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- FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques.—*J. Conch.*, Paris 88: 100–140.
- FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines.—*Archs Zool. exp. gén.* 74: 627–634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon.—*Ann. Mag. nat. Hist.* (13) 2: 309–320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean.—*Bull. Bingham oceanogr. Coll.* 17 (4): 1–51.
- THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269–270. Jena: Fischer.—*Denkschr. med.-naturw. Ges. Jena* 16: 269–270.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 69 Band
April 1976 April
Part 8 Deel



THE CRANIAL AND CERVICAL MUSCLES OF THE
SOUTH AFRICAN LIMBLESS LIZARD
TYPHLOSAURUS AURANTIACUS AURANTIACUS
PETERS (REPTILIA, SAURIA)

By

JURI A. VAN DEN HEEVER

Cape Town

Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
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Obtainable from the South African Museum, P.O. Box 61, Cape Town

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
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Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad

OUT OF PRINT/UIT DRUK

1, 2(1, 3, 5-8), 3(1-2, 4-5, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2), 10(1),
11(1-2, 5, 7, t.-p.i.), 15(5), 24(2), 27, 31(1-3), 33

Price of this part/Prys van hierdie deel
R3,80

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1976

ISBN 0 949940 87 9

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

THE CRANIAL AND CERVICAL MUSCLES OF THE SOUTH AFRICAN LIMBLESS LIZARD *TYPHLOSAURUS AURANTIACUS AURANTIACUS* PETERS (REPTILIA, SAURIA)

By

JURI A. VAN DEN HEEVER

South African Museum, Cape Town

(With 18 figures)

[MS accepted 25 November 1975]

ABSTRACT

The skull and cervical vertebrae of *Typhlosaurus aurantiacus aurantiacus* exhibit marked adaptations to a fossorial mode of life which is reflected in the associated musculature. Neither eye muscles nor supratemporal arches are present. The adductor musculature of the jaws, compacted into the temporal region, are dominated by two tripartite tendons, the bodenaponeurosis and the quadrate tendon. The m. pseudotemporalis is single. The m. cervicomandibularis is probably the major jaw opening muscle. Posttemporal fenestrae are absent and the cervical musculature encroaches far anteriorly on to the bulbous occiput. Discussed in terms of a lever of the third class the action of the jaw shows great similarity to that of a non-fossorial skink like *Mabuia*, and probably functions in an identical manner. Primary adaptations for a fossorial mode of life appear to be the strengthening and streamlining of the skull, loss of limbs and limb girdles and general attenuation of the body.

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INTRODUCTION

The doubtful taxonomic position of *Typhlosaurus* has been dealt with by various authors. Boulenger (1887) regarded the genus as related to *Acontias* but placed it, like Gadow (1901), together with *Anelytropsis* and *Feylinia* in the family Anelytropidae, close to the Scincidae. Camp (1923) places *Typhlosaurus*

in the Feyliniidae, within the superfamily Scincoidea, together with the Scincidae, the Anelytropsidae and the Dibamidae.

Hewitt (1929), De Witte & Laurent (1943) and FitzSimons (1943) also refer the genus to the Scincidae and according to Smit (in press) FitzSimons regards *Typhlosaurus* as derivable, via *Aconthophiops*, from *Acontias*. Romer (1956) rather doubtfully includes *Typhlosaurus* within the Scincidae. Greer (1970), on the basis of the external morphology and cranial osteology especially the relationship of the frontal bones and the bones of the secondary palate, regards *Acontias*, *Aconthophiops* and *Typhlosaurus* as a subfamily of the Scincidae, i.e. the Acontinae. Broadley (1968) agrees with FitzSimons and states: 'The genus *Typhlosaurus* appears to have been derived from an ancestral form of *Acontias*, after passing through an intermediate stage which is demonstrated by the monotypic genus *Aconthophiops*.' According to Smit (1964) the close relationship between *Typhlosaurus* and *Acontias* is abundantly confirmed by the cranial osteology of *T. caecus*, indicating that the genus *Typhlosaurus* undoubtedly belongs within the Scincidae.

The following classification is thus adopted.

- Class: Reptilia
- Order: Squamata
- Suborder: Sauria
- Family: Scincidae
- Subfamily: Acontinae Greer, 1968
- Genus: *Typhlosaurus* Wiegmann, 1834
- Species: *T. aurantiacus* Peters, 1882
- Subspecies: *T. aurantiacus aurantiacus* Broadley, 1968.

Limbless skinks of the genus *Typhlosaurus* are confined to southern Africa (Broadley 1968). Eight species were recorded by FitzSimons (1943), and one additional species, the greatly attenuated *T. braini* from the Namib Desert, was described by Haacke (1964). Subsequently Broadley (1968) revised the genus, recognizing eight species placed into three species groups.

The genus as a whole is fossorial and according to Mertens (1955) only appears on the surface towards evening. Their diet includes small insects and myriapods of which small beetle larvae and termites form the most important groups (Broadley 1968).

The cranial osteology of the fossorial Scincidae and forms with scincid affinities, such as *Dibamus*, are well known from the work done on *Acontias* (De Villiers 1939; Brock 1941; Van der Merwe 1944), *Dibamus* (Gasc 1968; De Weerd 1971), *Typhlosaurus* (Smit 1964), *Feylinia* (Du Toit 1971), *Typhlacontias* (Cluver 1965), *Melanoseps* (Boyd 1969) and *Scelotes* (Leonard 1973).

The postcranial skeleton is less well known and except for the work of Gasc (1967a, b, c; 1968) and Hofstetter & Gasc (1969) has attracted few investigators.

Myological studies on limbless lizards are few and far between. According to Auffenberg (1962) there is no record of the axial muscles of limbless lizards up to that time. Except for the work of Gasc (1968), De Weerd (1971) and Leonard (1973) the cranial muscles of limbless lizards are largely unknown. De Weerd's account differs from the more detailed description of Gasc. However, Gasc's description is difficult to evaluate in the light of comments given by Haas (1973), and Leonard discusses only the eye muscles in *Scelotes*.

Haas (1973) reviews the jaw muscles of the Rhynchocephalia and the Squamata stating that: '... detailed studies of the cranial muscles are lacking for two families (or groups often considered to be families) of lizards, namely the Anelytropsidae and the Feyliniidae'. Greer (1970) assigned these two groups to the Scincidae as the subfamilies Acontinae and Feylininae. Together they represent the fossorial Scincidae of which the above statement is certainly true.

The previously mentioned studies have shown that a fossorial habit produces distinctive skeletal changes. Change in skeletal proportions should inevitably affect associated musculature and in view of this fact the acute lack of literature on the myology of fossorial Scincidae is believed to sufficiently justify this paper.

MATERIAL AND METHODS

Three alcohol-fixed specimens of *Typhlosaurus aurantiacus* were obtained from the South African Museum. One specimen was dissected and the skull and postcranial skeleton were used for comparative and photographic purposes. Both the other specimens were decalcified for a period of seven days in 7.5 per cent solution of nitric acid in 70 per cent alcohol. Subsequently the specimens were separately dehydrated, cleared in terpineol and embedded in paraffin wax (52–54°C). Sectioned at 20 microns, one specimen gave excellent results; the other proved of no use and was discarded. Staining and counter-staining were done with the azocarmine-azan method and the enlarged drawings of the sections were made with the aid of a camera lucida microscope attachment.

Owing to the paucity of material several specimens of the related but more abundant genus *Acontias* were dissected to elucidate gross topography.

DESCRIPTION

OSTEOLOGY

Cranial osteology

The skull of *Typhlosaurus caecus*, which closely resembles that of *T. aurantiacus*, was described by Smit (1964), and the reader is referred to this paper for a comprehensive account of the cranial osteology. However, prior to embarking on a description of the myology, the cranial and the cervical osteology merit a few additional remarks on certain areas important to muscle attachments, where Smit's description is inadequate for the purpose of this paper.

T. aurantiacus has the elongate skull and reduced orbits common to attenuate fossorial lizards (Figs 1A-B, 2A). The eyes are visible as inconspicuous black dots through the transparent integument and are devoid of associated musculature. However, an optic nerve is present and the retinal pattern resembles

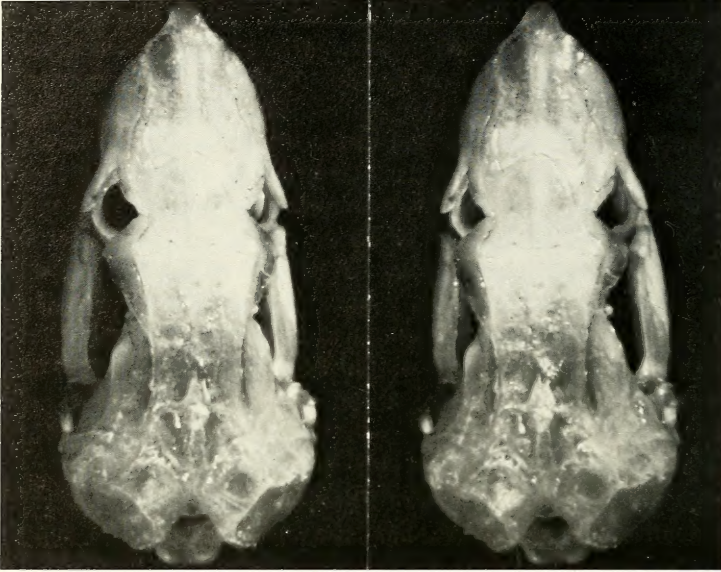


Fig. 1A. Stereophotographs of *Typhlosaurus aurantiacus* skull; dorsal view.

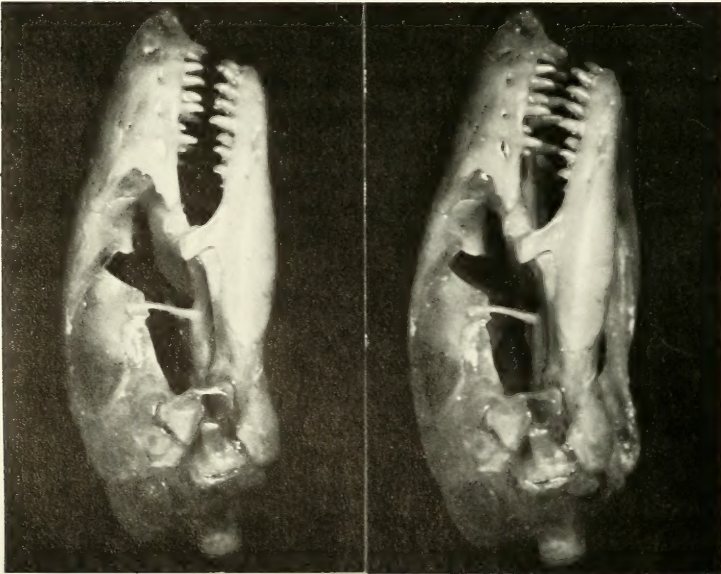


Fig. 1B. Stereophotographs of *Typhlosaurus aurantiacus* skull; lateral view.

that of amphisbaenids, in which light perception has been demonstrated by Bonin (1965).

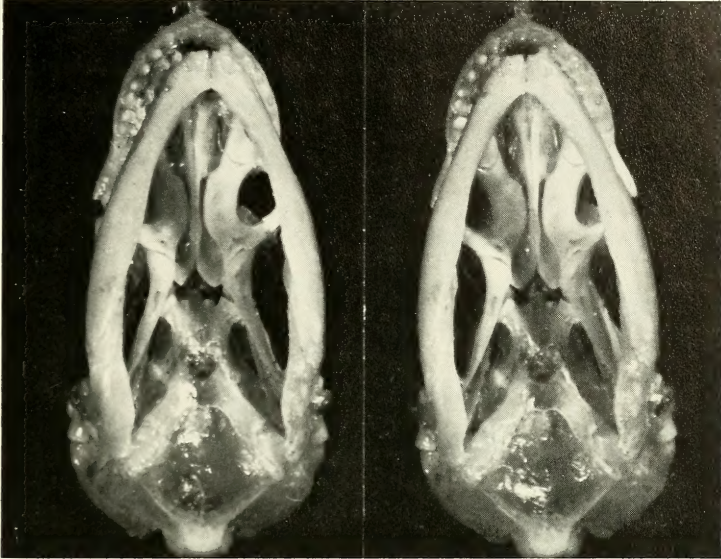


Fig. 2A. Stereophotographs of *Typhlosaurus aurantiacus* skull; ventral view.

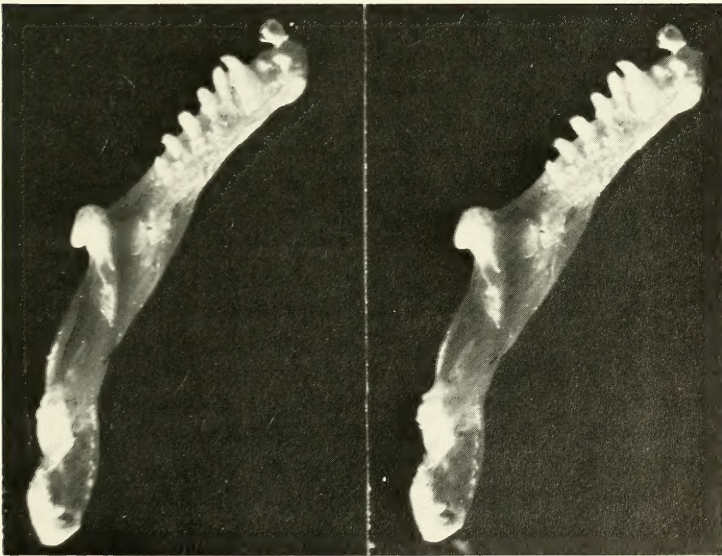


Fig. 2B. Stereophotographs of *Typhlosaurus aurantiacus* lower jaw;
lingual view.

No remnants of lacrimal bones were found. The supratemporal arch is absent but both the squamosal and supratemporal bones are present as small, flattened, slightly overlapping elements dorsal to the quadrate.

The squamosal, lying anterolateral to the supratemporal, is tendinously connected to the quadrate head (Figs 3, 13). The supratemporal lies postero-medial to the squamosal and shares with the much reduced paroccipital process of the otic capsule the articulation with the quadrate head by means of a pad of fibrocartilage (Fig. 3).

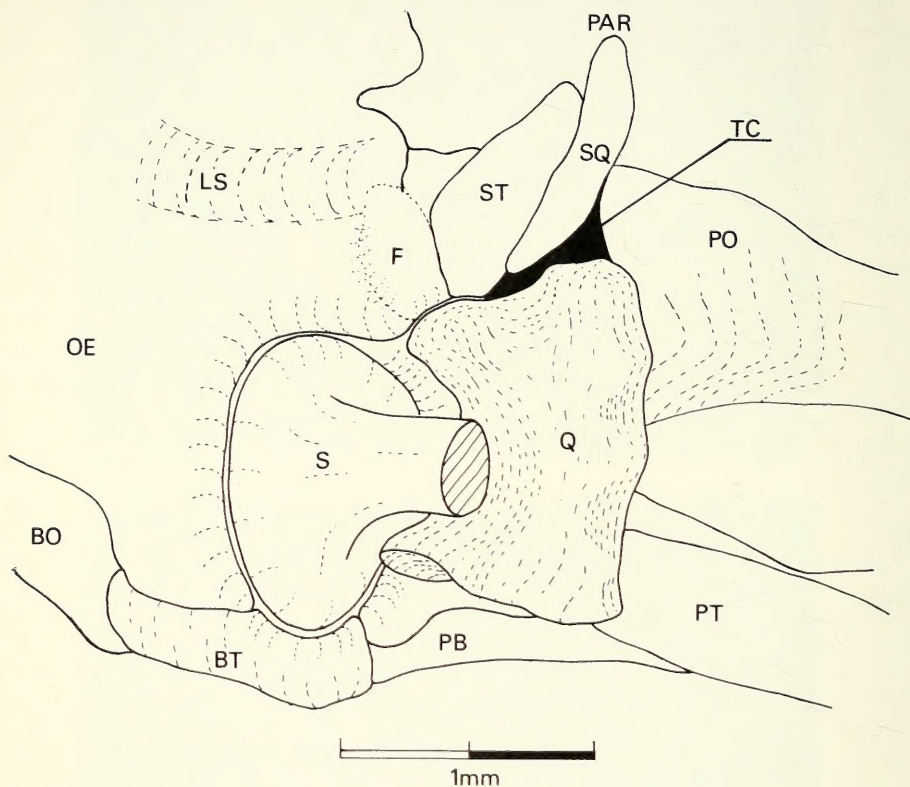


Fig. 3. Posterolateral view of the skull.

The proportions of the posterior half of the skull are of importance. The temporal region, where the adductor musculature is accommodated, is laterally compressed and the otico-occipital region is much expanded both laterally and posteriorly (Figs 1A-B, 2A). These relations create the impression that the suspensorium is more anteriorly located than in a non-fossorial lizard such as *Mabuia*. The entire posterior border of the parietal meets the supraoccipital and the fused exoccipital-opisthotic complex in a dorsally lying suture. There is thus no posttemporal fenestra and the back of the skull is smooth and bluntly

rounded (Fig. 1A). Immediately below the foramen magnum a kidney-shaped condyle is present, composed laterally of the exoccipitals and medially of a suturely distinct basioccipital bone. Ventrally the basioccipital forms the posterior portion of the skull base, curving upwards to meet the exoccipital ventrolaterally to the condyle.

A tympanum and middle ear cavity are absent. The columella is massive, consisting of a large footplate and a short anterolaterally directed stapes (Figs 3–4), which extends laterally beyond the quadrate as a rod-like cartilaginous extracolumella, terminating a short distance anterior to the quadrate

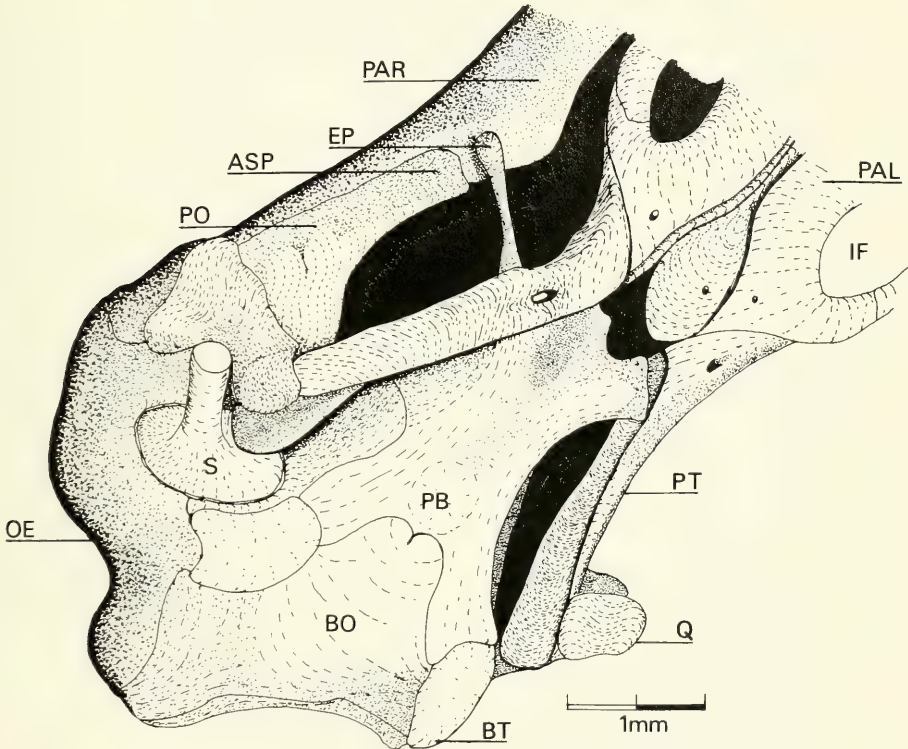


Fig. 4. Posteroventral view of the skull.

and ventrolateral to the medius portion of the external adductor muscle (Figs 5, 7–8, 12–13). The tendinous sheath surrounding the extracolumella is joined to the retroarticular process of the lower jaw as in *Typhlosaurus caecus* (Smit 1964) and *Acontias meleagris* (De Villiers 1939; Brock 1941; Van der Merwe 1944), and is suspended anteriorly by a ribbon of fascia overlying the tendinous covering of the adductor musculature and attaching to the dorsolateral border of the parietal (Figs 5, 7–8, 12). The same condition exists in *T. caecus* and *T. lineatus*.

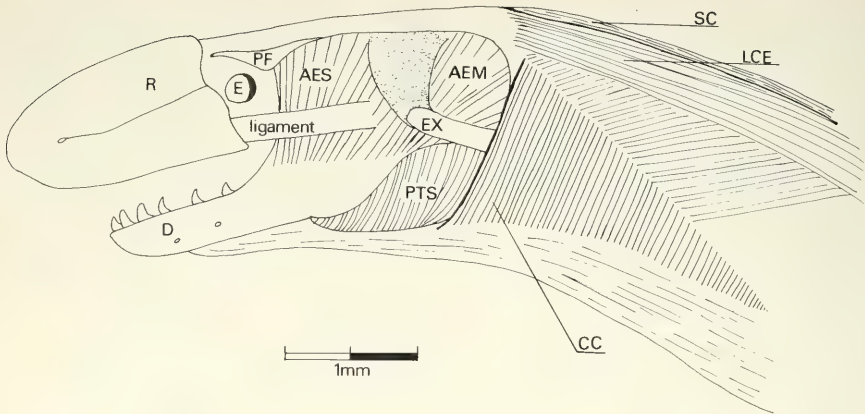


Fig. 5. Lateral superficial view of musculature.

The quadrate ramus of the pterygoid is gutter-shaped, with the trough directed medially in the region of the basipterygoid joint to receive the basipterygoid process. Posteriorly the quadrate ramus is twisted through ninety degrees so that the trough faces ventrally where the posterolateral extremity of the bone is tendinously connected to the ventromedial surface of the quadrate (Fig. 4).

The anterior border of the quadrate is gently rounded for the attachment of the lateral lamina of the quadrate tendon, while the posterior border of the bone is concave to accommodate the laterally protruding stapes (Fig. 3). Ventrally the large quadrate condyle articulates synovially with the lower jaw. Dorsal to the attachment of the quadrate ramus of the pterygoid the medial surface of the quadrate is slightly concave to accommodate the origin of the posterior adductor muscle (Fig. 13). Dorsally the posterior part of the quadrate head articulates synovially with both the supratemporal and the otic capsule (Figs 3, 14).

The anterior part of the quadrate head is separated from the cranium by fibres of the medius portion of the external adductor muscle and serves for the origin of the vertical lamina of the quadrate tendon. The central part of the quadrate head is tendinously attached to the squamosal (Figs 3, 13).

The thin, rod-like epipterygoid fits ventrally into the columellar fossa on the dorsal surface of the pterygoid, lateral to the basipterygoid joint. Both condylar surfaces are capped by cartilage. The dorsal extremity of the bone attaches tendinously to the lateral surface of the parietal downgrowth immediately in front of the anterior superior process of the pro-otic (Fig. 4).

Because of the importance of the mandibular muscle insertions it is necessary to augment the brief description of Smit (1964) of the lower jaw of *Typhlosaurus caecus*. Each ramus consists of the normal six bones, viz. dentary, coronoid, splenial, surangular, angular and a fused articular-prearticular, to

which the surangular is also partially fused (Fig. 17). Between the coronoid process and the glenoid fossa both dentary and surangular bulge laterally, forming a dorsolateral mandibular shelf on to which elements of the adductor musculature insert (Fig. 11). Posteriorly, at the insertion of the pterygomandibularis muscle, the ventral border of the jaw is concave (Fig. 17).

The dentary extends from the symphysis to the supra-angular foramen and constitutes the anterior portion of the mandibular shelf (Figs 9–10). It carries eight to nine pleurodont teeth, contributes the lateral half of the coronoid process and is medially recessed along its posterior half to accommodate the remaining lower jaw bones (Fig. 17). It is pierced laterally and antero-ventrally below the tooth row by a line of four mental foramina, and postero-medially by a large foramen transmitting the anterior mylohyoid nerve and the lingual branch of the inferior alveolar nerve; anteromedially there are foramina for the Meckelian cartilage and the anterior tip of the inferior alveolar nerve. The position of the posteromedial foramen varied in the two *Typhlosaurus aurantiacus* specimens investigated. In the serially sectioned skull the anterior process of the coronoid bone and the anterior tip of the splenial form the posterior border of the foramen, whereas, in the cleared specimen, the foramen lies well within the boundaries of the dentary (Fig. 17). Behind the coronoid process, fibres of the posterior adductor muscle and the medius portion of the external adductor muscle insert along the dorsolateral border of the dentary.

The coronoid lies midway along the mandible, flattened medially against the dentary, prearticular and surangular. Its coronoid process is a prominent vertical sheet lying against the coronoid process of the dentary (Figs 2B, 9). Ventrally the bone is braced against the action of the adductor muscles by an anterior and a posterior process, the former bridging the dentary-prearticular suture and the latter the surangular-prearticular suture (Fig. 17). Two parallel, near-vertical grooves are present on the trailing edge of the coronoid process. Separated by a ridge, they continue posteroventrally on to the medial side of the posterior process; the more lateral of the two grooves receives the insertion of the medius portion of the external adductor muscle while the pseudotemporalis muscle inserts into the medial groove (Figs 10, 17).

The surangular (Figs 9–12, 17) lies posteromedially to the dentary, posterolaterally to the coronoid, dorsally to the prearticular and anteriorly to the articular. Laterally it forms the posterior section of the mandibular shelf (Fig. 11) and dorsally it bears a ridge extending between the coronoid and the articular processes. Its anterior extremity underlies the coronoid process while in addition to covering the Meckelian canal up to the adductor fossa, the posterodorsal tip of the bone constitutes the anterior part of the articular process. Posteromedially the bone forms the dorsal border of the adductor fossa and is laterally pierced by the posterior supra-angular foramen, which leads from the adductor fossa, and the anterior supra-angular foramen which leads from the Meckelian canal. The posterior adductor muscle and medius portion of the external adductor muscle insert on the dorsomedial and dorso-

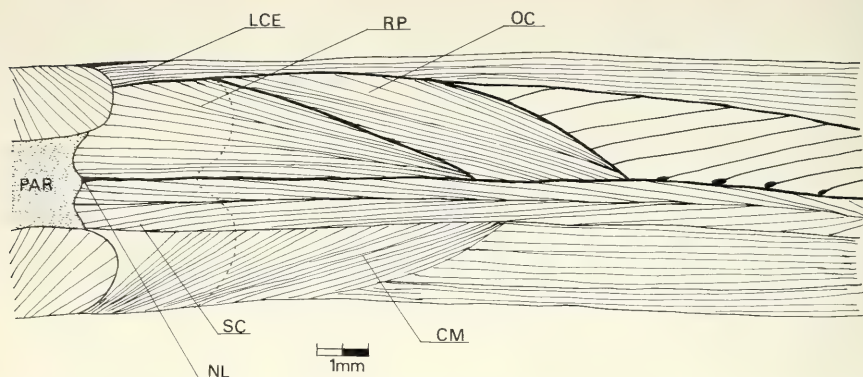


Fig. 6. Dorsal superficial view of the cervical musculature; spinalis capitis muscle removed on the right side.

lateral surfaces of the surangular. Posteriorly the bone is fused to the articular-prearticular complex.

The splenial (Figs 9–10) is a thin sliver of bone on the inner surface of the jaw in line with the coronoid process. It lies posteromedially to the dentary, medially to the prearticular, dorsally to the angular and ventrally to the coronoid. It is devoid of any muscle insertions and neither bears foramina nor contributes to the inner wall of the Meckelian canal.

The angular (Figs 9–10, 11, 17), a narrow ventral element below the prearticular and splenial, lies with its anterior tip within the dental recess and traverses the jaw posteroventrally between the prearticular and dentary to terminate posteriorly on the lateral surface of the mandible, ventral to the posterior tip of the surangular. Between the prearticular and dentary it forms a narrow medial section of the floor of the Meckelian canal, from the adductor fossa to immediately anterior to the coronoid process. At its midpoint it is pierced ventrally by the posterior mylohyoid foramen, which transmits the posterior mylohyoid nerve.

The prearticular (Figs 11–12, 17) lies ventrally to the surangular, posteromedially to the dentary, dorsally to the angular and laterally to the coronoid and the splenial. It forms most of the medial wall and part of the floor of the Meckelian canal as well as the ventral border of the adductor fossa. Medially it receives the insertion of the adductor musculature and posteriorly it is completely fused to the articular.

Behind the glenoid fossa the articular-prearticular (Figs 13–17) forms the spoon-shaped retroarticular process, which receives the insertion of the pterygoideus muscle on its medial and lateral surfaces and that of the depressor mandibulae muscle on the dorsal surface. The glenoid fossa, lined with cartilage, lies in front of the insertion of the depressor mandibulae muscle and behind and against the articular process. The foramen for the chorda tympani lies medially on the retroarticular process, with its canal extending anteriorly through the

bone to open into the adductor fossa.

The hyoid apparatus in *Typhlosaurus aurantiacus* is a triradiate, cartilaginous structure resembling a tuning-fork with posteriorly divergent prongs. It lies ventral to the trachea and extends posteriorly from the glottis to a point in line with the posterior border of the pterygoideus muscle. Anteriorly, in the ventral midline, the lingual process (proc. entoglossus) supports the tongue musculature (Figs 9–10).

No part of the hyoid apparatus is ossified and the structure could consequently not be divided with certainty into the various components commonly found in reptiles. From the work of Van der Merwe (1944), Langebartel (1968) and De Weerd (1971) it appears that the paired posterior prongs represent the first ceratobranchials.

Cervical osteology

Vertebrae and ribs are highly variable structures and in the limbless squamates the regional differentiation of the vertebral column has led to various interpretations of the cervical vertebrae. Zangerl (1945) recognizes four vertebral divisions in the Amphisbaenidae, i.e. cervical, thoraco-lumbar, cloacal and caudal. The cervical region includes all the anterior ribless vertebrae, i.e. atlas, axis and one to two of the following vertebrae, whilst the thoraco-lumbar region includes all vertebrae with movable unforked ribs. Sood (1948) divides the ophidian vertebral column into a precaudal and a caudal region of which the former is subdivided into cervical, thoracic and lumbar sub-regions. The cervical sub-region consists only of the atlas and the axis whereas the thoracic region includes all vertebrae following the axis and which bear hypapophyses. List's (1966) description of the burrowing snakes follows Zangerl (1945) in defining the regions of the vertebral column. Consequently he defines the cervical region in burrowing snakes as consisting only of the atlas and the axis since the vertebrae following the axis bear unforked ribs and are therefore included in the thoraco-lumbar region. List notes that although this system appears satisfactory for the Typhlopidae and Leptotyphlopidae its use is limited in that it cannot be directly applied to other vertebrates.

According to Gasc (1968) and Hofstetter & Gasc (1969) the cervical vertebrae can only be defined as those vertebrae preceding the vertebrae carrying the first rib attached to the sternum. These authors refer to the work of Stannius (1849) and state that all other definitions of cervical vertebrae such as ribless anterior vertebrae, vertebrae with hypapophyses or ribless vertebrae plus vertebrae with short ribs are invalid because too many exceptions and contradictions are involved.

Limb regression is usually accompanied by regression of the girdles and in certain of the fossorial Scincidae, e.g. in the genus *Typhlosaurus*, this phenomenon is rather pronounced. In *Feylinia* the ribs of the eighth vertebra are still attached to a vestigial sternum (Gasc 1965), in *Dibamus* the pectoral girdle is connected to the fifth vertebra (Gasc 1968) and in *Acontias meleagris* the

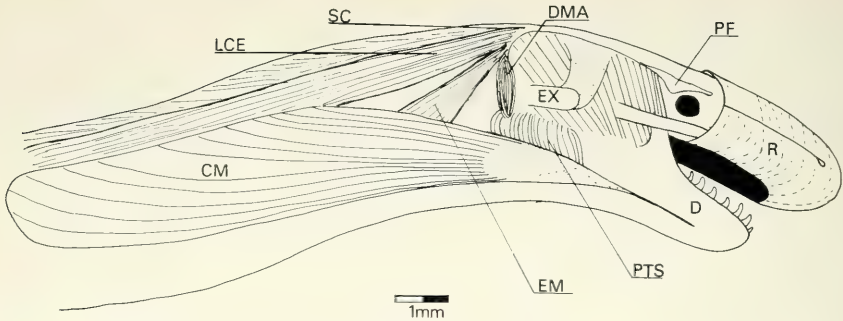


Fig. 7. Ventrolateral view of the superficial neck musculature.

vestigial girdle is united by the serratus muscle to the second and the third ribs. In *T. vermis* the pectoral girdle is absent (Hofstetter & Gasc 1969). In *T. aurantiacus* the pectoral girdle is also absent, and the ribs consequently lack sternal attachments. It is therefore not possible to define a specific cervical region within the vertebral column of *T. aurantiacus*. In limbless squamates such as ophidians (completely lacking a pectoral girdle) and amphisbaenids (lacking sternal attachments of the ribs) Hofstetter & Gasc (1969) divide the vertebral column into preloacal, cloacal and caudal regions.

In this paper the term 'cervical' does not define a region of the vertebral column but refers only to that area on the preloacal region of the vertebral column from which the musculature responsible for the movements of the head arise.

Typhlosaurus aurantiacus has procoelous vertebrae as in all saurians except the Gekkonidae. The broad elliptical condyles are slightly dorsally orientated and are as wide as the centra of the vertebrae. The first pairs of ribs are carried by the third vertebra, as in *Acontias meleagris*.

The ribs are holocephalous (unicipital) and each has two tuberculiform processes close to the costal head; one anteroventrally and one postero-dorsally for the attachment of the intercostal muscles. A similar condition exists in *T. vermis* (Hofstetter & Gasc 1969). As a result of the increased functional importance of the cervical musculature in a limbless burrower such as *T. aurantiacus*, the synapophysis of the axis and the following three vertebrae are laterally extended to enlarge the area of origin of the cervical musculature.

The atlas consists of paired neural arches and a ventral intercentrum. A neural spine is absent and the two semilunate neural arches do not fuse dorsally. No functional zygapophyses are present between the atlas and the axis, although the atlas has a small process on the posterolateral margin of the neural arch in a similar position to the postzygapophyses of the other vertebrae.

The axial centrum bears two hypapophyses, of which the posterior one is probably derived from the intercentrum of the third vertebra as Holder (1960) found in gekkos. Anterolaterally the neural arch has a small process

coinciding with the position of the prezygapophyses on the vertebrae following the axis. The neural spine resembles the blade of an axe and extends the full length of the neural arch.

Midventrally on the centra of each of the seven vertebrae following the axis a hypapophysis is present. The neural spines, posterodorsally situated on the neural arches, extend obliquely caudally. The vertebrae articulate by

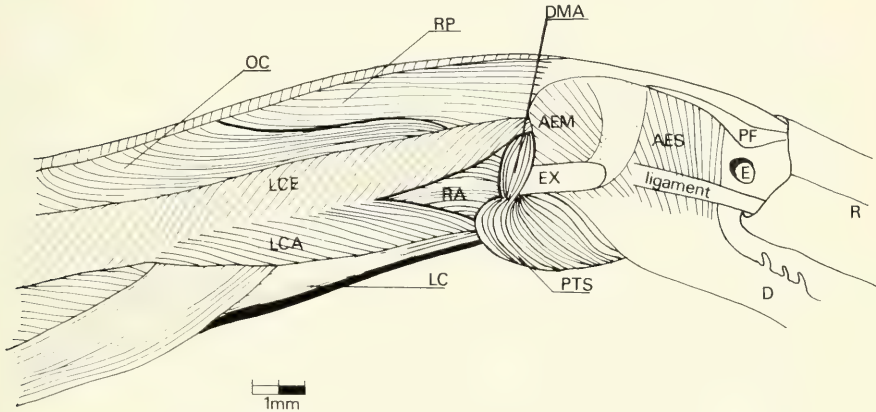


Fig. 8. Lateral view of the deep cervical musculature.

means of pre- and post-zygapophyseal processes and no zygosphenes-zygantrum type of articulation, as found in snakes and some saurian families, is present in *Typhlosaurus aurantiacus*.

MYOLOGY

Muscle classification and nomenclature

The currently accepted classification of visceral cranial muscles is based on Vetter's (1874, 1878) and Ruge's (1897) studies on selachians. The Constrictor superficialis (Cs) is subdivided into segmentally innervated portions, i.e. the trigeminus muscle complex as the Constrictor superficialis I (Cs₁); the facial muscles as the Constrictor superficialis II (Cs₂); the glossopharyngeal muscles as the Constrictor superficialis III (Cs₃); and the vagus muscles as the Constrictor superficialis IV–VIII (Cs_{4–8}). Luther (1914) extended this classification to tetrapods and introduced a subdivision of the jaw adductors based on the spatial relationships of the muscles with the three rami of the trigeminal nerve. This system has been generally accepted for sauropsids by most authors including Adams (1919), Lakjer (1926), Haas (1930, 1934, 1973), Lubosch (1933), Edgeworth (1935), Brock (1941), S  ve-S  derbergh (1945), Ingeborg Poglayen-Neuwall (1953, 1954), Ivo Poglayen-Neuwall (1953a, 1953b), Oelrich (1956), Ostrom (1961), Gasc (1968) and Barghusen (1973). In sauropsids the Constrictor I is divided into the m. constrictor I dorsalis (M.C_{1d}), the m. constrictor I

lateralis (M.C₁l) represented by the m. adductor mandibulae, and a m. constrictor I ventralis (M.C₁v), the m. intermandibularis.

The constrictor I dorsalis (M.C₁d) extends between the cranium and the movable palatal complex. This group of muscles is involved with kinetic movements of the skull and they are variable in their occurrence.

Basically, the constrictor I lateralis (M.C₁l), the m. adductor mandibulae of sauropsids, is divided into an external, and internal and a posterior muscle. The external adductor is usually subdivided into three portions, i.e. superficialis, medius and profundus. The internal adductor commonly consists of two, well-separated muscles, the m. pseudotemporalis and the m. pterygoideus. The posterior adductor is usually a single muscle.

The constrictor I ventralis (M.C₁v), the m. intermandibularis, is situated between the rami of the lower jaws, superficial to the throat musculature, and is subdivided into an anterior and a posterior portion.

Lubosch (1933) recognizes three basic arrangements of jaw muscles, i.e. selachian, amphibian and mammalian, of which the jaw muscles of sauropsids belong to the amphibian type. Homologies between the three types are uncertain, according to Haas (1973), and are further complicated by the varied nomenclature in existence for saurian jaw musculature. For a complete list of synonyms see Lakjer (1926), Edgeworth (1935) and Haas (1973).

Nishi (1919) laid down the terminology for axial musculature and, together with Vallois (1922), is amongst the few workers who have approached axial musculature on a comparative basis. More recent accounts are those of Olson (1936) and Evans (1939).

Reptilian epaxial musculature is divisible into three longitudinal systems. Dorsomedially the transversospinalis system lies lateral to the spinous processes of the vertebrae, the longissimus system lies lateral to the transversospinalis system and dorsal to the heads of the ribs, and the iliocostalis system lies on the ribs dorsal to the upper margin of the external oblique abdominal muscles. Anteriorly, towards the occiput, the epaxial musculature breaks down into various shorter groups of fibres, the cervical muscles, which insert posteriorly on to the skull and are responsible for the movements of the head.

The hypaxial musculature does not fall within the scope of this paper.

Constrictor dorsalis group (C₁d)

This group of muscles lies deep to the adductor musculature and is responsible for the intercranial kinetic movements of the skull. The muscles arise, in Versluys' (1912) terminology, on the occipital segment of the skull and insert on to the maxillary segment. In *Typhlosaurus aurantiacus* the group is represented by a minute m. levator pterygoidei and a large m. protractor pterygoidei. A levator bulbi muscle is absent.

The small m. levator pterygoidei (lp, Figs 9-10), roughly triangular in transverse section, lies laterally to the basiptyergoid joint, the opthalmic ramus of the trigeminal nerve, the palatine ramus of the facial nerve, the internal

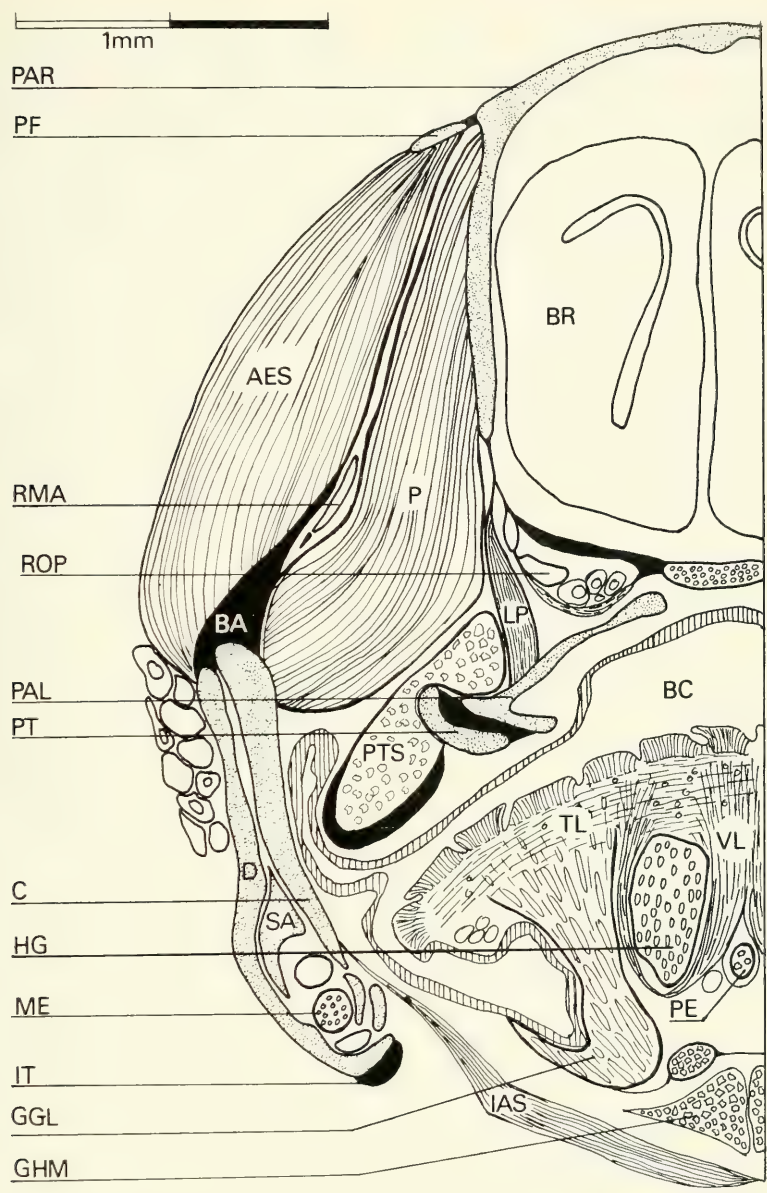


Fig. 9. Cross-section of the skull at the level of the coronoid process.

carotid artery and the origin of the protractor pterygoidei muscle; medially to the pseudotemporalis muscle, the anterior part of the pterygoideus muscle and the epipterygoid. It lies against the medial surface of the epipterygoid with the posterior border of the muscle in line with that of the bone.

The muscle arises as a ribbon of fascia from the lateral surface of the pro-otic membrane, ventral to the lateral parietal downgrowth, medioventral to the dorsal extremity of the epipterygoid bone and anteroventral to the anterior superior process of the pro-otic.

The insertion is fleshy and bridges the palatine-pterygoid suture dorsally. Anteriorly it attaches on to the posterolateral border of the palatine bone, medially to the anterior extremity of the pterygoideus muscle, and posteriorly it attaches on to the anterodorsal surface of the pterygoid bone medially to the columellar fossa.

A nerve seen within the muscle in transverse section was too small for its connections to be traced.

The large m. protractor pterygoidei (prp, Figs 11–14) lies behind the basipterygoid process, the individual fibres extending obliquely between the lateral margin of the skull base and the full length of the quadrate ramus of the pterygoid. The muscle is situated posteromedially to the levator pterygoidei muscle, medially to the mandibular ramus of V, dorsally to the pterygoideus muscle, ventrally to the Gasserian ganglion and the proximal part of the ophthalmic ramus, and laterally to the parasphenoid-basisphenoid complex, the otic capsule, the palatine ramus of VII, and the internal carotid artery.

The muscle arises fleshily from the dorsal surface of the basipterygoid process, the lateral surfaces of the parasphenoid-basisphenoid complex and the anterior inferior process of the pro-otic, and anteroventrally from the lateral surface of the pro-otic proper (Figs 9–11). Anteroventrally within the muscle a flat tendon is present which arises ventrally on the basipterygoid process. Fibres arise from both dorsal and ventral surfaces of the tendon.

The insertion is confined to the quadrate ramus of the pterygoid bone posterior to the basipterygoid process. Fibres insert along the inner concave surface and the dorsal surface of the ramus. An insertional tendon is present within the muscle, posterodorsally to the tendon of origin, the fibres insert on to its dorsal and ventral surfaces. This tendon attaches to the dorsal (inner) rim of the quadrate ramus (Figs 11–12).

The muscle is innervated by a separate branch of V leaving the Gasserian ganglion ventrally, piercing the muscle dorsally and coursing anteriorly a short distance before ramifying.

Adductor mandibulae group

Compared with non-fossorial lizards, the adductor musculature as exemplified by *Typhlosaurus aurantiacus* is modified to function as a compact unit within the temporal indentation. The external adductors are dominated by two oblique, parallel tendons, of which the anterodorsal one is a modified bodenaponeurosis. It arises as a single tendon on the coronoid process of the lower jaw (Fig. 9), posterior to which it fans out into the external adductor mass as three laminae. In transverse section this unit appears as a tripartite structure resembling an inverted Y (Fig. 11). The three laminae serve as areas of insertion to the external

and internal adductors and will be referred to in the text as the vertical, medial and lateral laminae of the bodenaponeurosis.

The second tendon (Figs 11–12), located posteroventrally to the bodenaponeurosis, also shows a tripartite configuration. It arises on the quadrate and extends anteroventrally to just posterior to the base of the coronoid process. This tendon will be referred to as the quadrate tendon and its laminae as the vertical, medial and lateral laminae of the quadrate tendon. Each lamina has a separate origin from the quadrate. The vertical lamina arises from the dorsal midline of the quadrate, piercing the medius portion of the external adductor muscle ventromedially. The lateral lamina arises from the anterior border of the bone and the medial lamina along its inner dorsal surface (Fig. 13), covering the medial surface of the posterior adductor fibres arising from the medial surface of the quadrate.

Ventrolaterally to the superficial portion of the external adductor and anteromedially to the extracolumella, a ligament is present in the position of the quadrato-maxillary ligament as described by Ingeborg Poglayen-Neuwall (1953) and Haas (1960). In *Typhlosaurus aurantiacus*, however, this ligament arises ventrolaterally from the lateral lamina of the bodenaponeurosis and extends anteriorly within the upper lip (Figs 5, 7–8), terminating laterally to the premaxillary. Ventrolaterally to the orbit the integument turns under this ligament to form the angle of the mouth.

A small horizontal bundle of muscle fibres is associated with the extracolumella (Fig. 12). It lies in a somewhat similar position to the m. retractor anguli oris of the amphisbaenids *Amphisbaena* and *Leposternon* as described by Lakjer (1926). However, in *Typhlosaurus aurantiacus* these fibres extend between the anteromedial surface of the extracolumella and the lateral lamina of the bodenaponeurosis and they apparently function to draw the extracolumella against the lateral surface of the adductor musculature.

The three major divisions of the adductor mandibulae group are readily identified by virtue of their spatial relationship with the three rami of the trigeminal nerve (Luther 1914). In *Typhlosaurus aurantiacus* the external adductor muscle mass lies laterally to the maxillary and mandibular rami (Figs 10–12), the internal adductor lies medially to the maxillary but laterally to the ophthalmic rami (Fig. 9), and the adductor posterior lies laterally to the mandibular ramus and ventrally to the external adductor (Fig. 12).

Musculus adductor mandibulae externus

The external adductor musculature arises within the temporal indentation and its origin is bordered dorsally by a curved ridge on the parietal, extending from the posterior tip of the postfrontal to the posterior extremity of the parietal (Figs 9–14).

Three portions of the external adductor musculature—the superficialis, medius and profundus—are present, either separated by tendinous laminae or by differences in fibre orientation.

The musculus adductor mandibulae externus superficialis (aes, Figs 9–11), the most lateral portion of the external adductor, lies partially anterior to the medius and profundus portions. Posteriorly, it is separated from them by, respec-

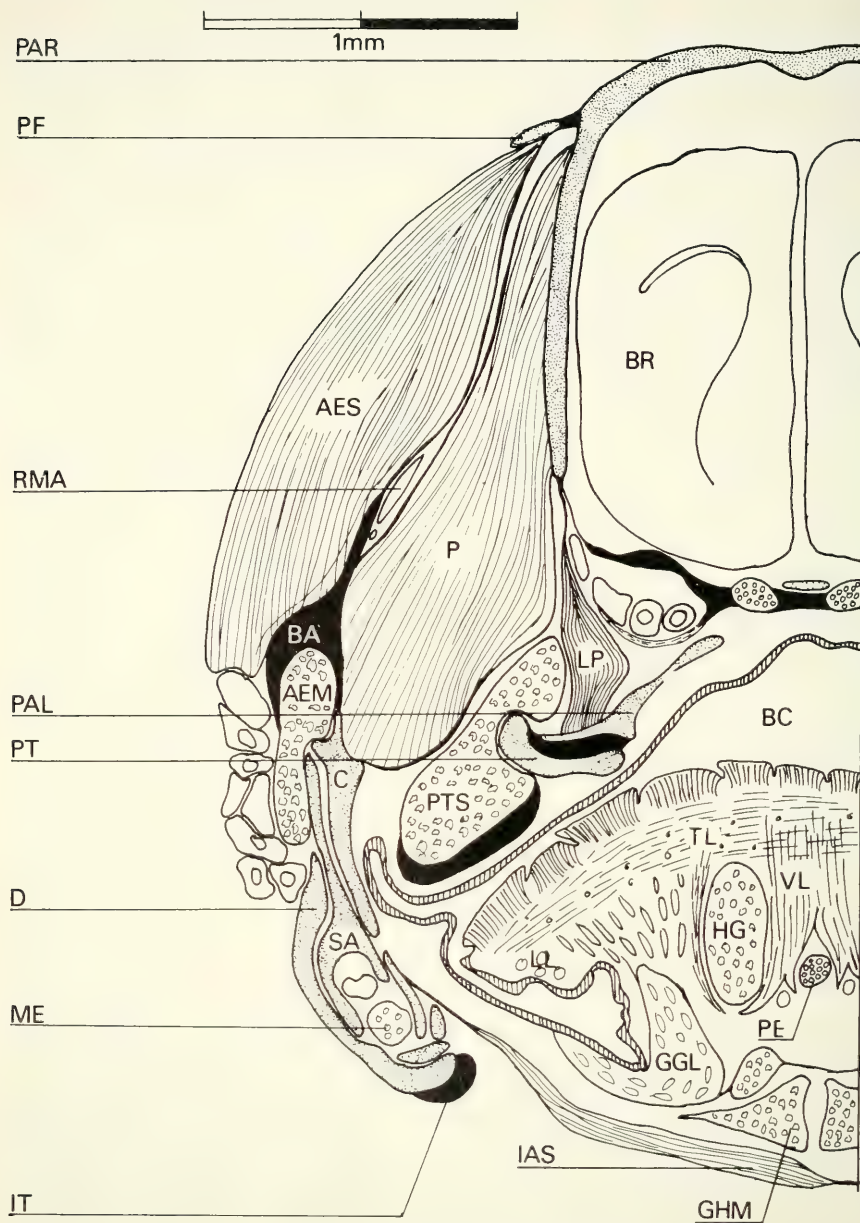


Fig. 10. Cross-section of the skull just behind Figure 9.

tively, the lateral and the vertical laminae of the bodenaponeurosis. Anteriorly the superficialis lies lateral to the pseudotemporalis muscle and is separated from it by the maxillary ramus of the trigeminal nerve. Dorsal to the vertical lamina of the bodenaponeurosis there is no distinction, other than fibre orientation, between the superficialis and profundus portions. The superficialis, however, is readily identified by the dorsoventral arrangement of its fibres as opposed to the anteroventral orientation of the profundus fibres. The two portions are by no means confluent since they separate easily during dissection. The most substantial part of the superficialis lies dorsal to the coronoid process, resulting in a near vertical fibre orientation relative to the long axis of the lower jaw (Fig. 9).

The superficialis portion arises from the ventral surface of the postfrontal (Fig. 9), from the dorsolateral ridge on the parietal (Fig. 11) and from the lateral surface of the profundus portion. The origins are fleshy throughout.

Insertion is effected laterally on to the vertical and lateral laminae of the bodenaponeurosis (Fig. 9), from the coronoid process posteriorly to a point dorsal to and almost in line with the anterior tip of the extracolumella.

The superficialis portion is innervated by a posterolateral branch of the mandibular ramus of V, which runs anterodorsally through the medius portion to enter the medial surface of the superficialis portion via the medial lamina of the bodenaponeurosis.

The *musculus adductor mandibulae externus medius* (aem, Figs 11–14) lies posterolaterally to the pseudotemporalis muscle and between the bodenaponeurosis and the quadrate tendon, with the vertical lamina of the latter piercing it along the ventromedial border. It extends anteroventrally from the posterolateral border of the parietal to the lower jaw and, being the most ventral portion of the external adductor muscle, its dorsal border is wedged between the lower extremities of the superficialis and profundus portions, separated from them by, respectively, the lateral and medial laminae of the bodenaponeurosis. Ventrally the muscle is forked, straddling the lower jaw from the coronoid process to the anterior border of the posterior adductor muscle. At this point there is, for a short distance, no partition between the fibres of the medius portion of the external adductor and those of the posterior adductor (Fig. 11). However, the medius portion is distinctly separated from the posterior adductor by the lateral and medial laminae of the quadrate tendon over practically its entire length. Posterior to the bodenaponeurosis and dorsal to the quadrate, the medius fibres are continuous with those of the more medially situated profundus portion of the external adductor (Fig. 12). It can, however, be determined with reasonable accuracy that most of the fibres in this area belong to the medius portion.

The medius portion arises fleshily from the posterolateral surface of the parietal (Fig. 12), the lateral surfaces of the supratemporal, the squamosal, the pro-otic dorsal to the quadrate and the lateral surface of the quadrate above the extracolumella (Fig. 13).

The insertion remains fleshy throughout and the fibres attach on to the inferior surfaces of the medial and lateral laminae of the bodenaponeurosis, the superior surfaces of the medial and lateral laminae of the quadrate tendon, the medial and lateral surfaces of the vertical lamina of the quadrate tendon, and into

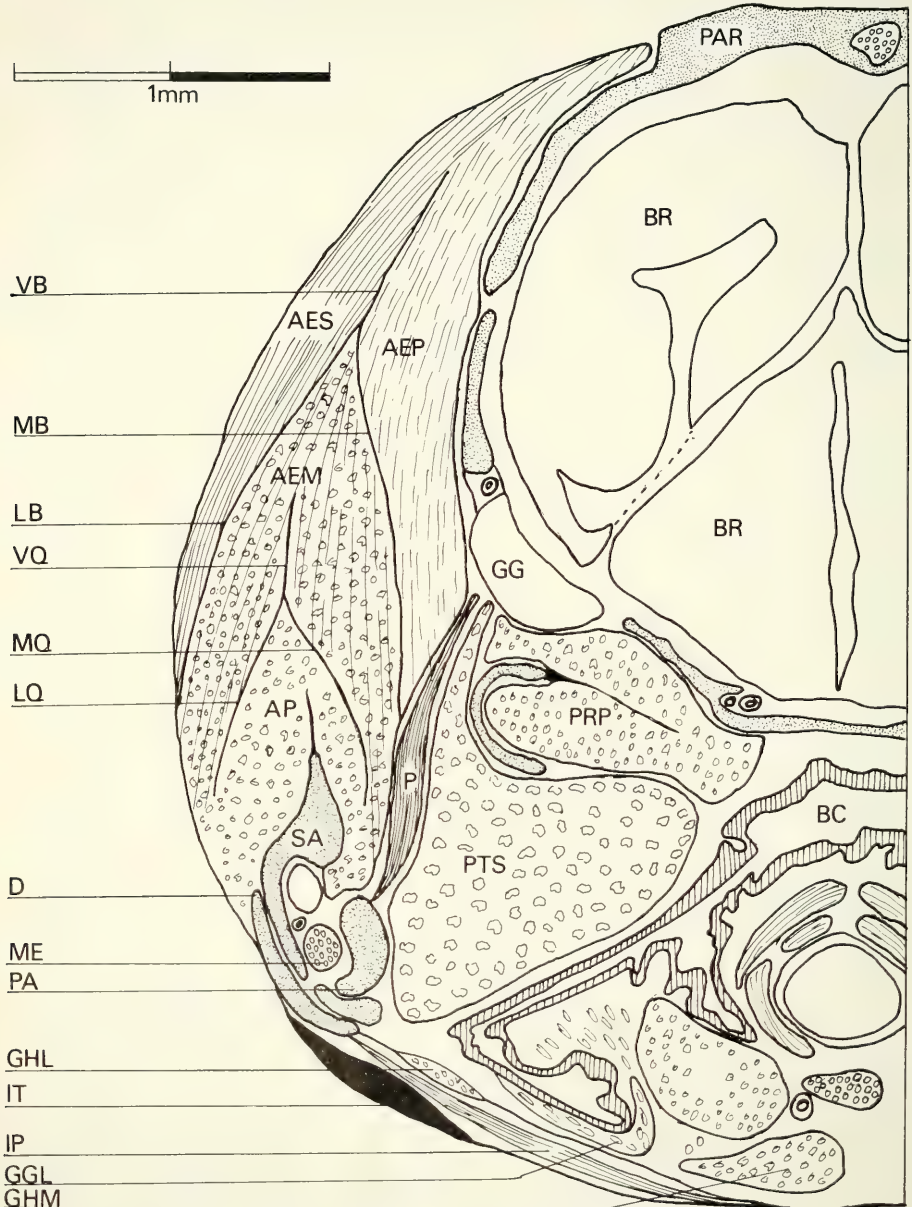


Fig. 11. Cross-section of the skull at the level of the Gasserian ganglion.

the lateral groove on the coronoid (Fig. 10), with a few fibres attaching posterolaterally on to the coronoid process of the dentary. Between the base of the coronoid process and the foramen for the anterior supra-angular nerve, the insertion utilizes the medial surface of the surangular, the dorsomedial surface of the posterior process of the coronoid and a small dorsomedial area on the prearticular, anterior to the adductor fossa. Dorsally the insertion continues along the surangular ridge, anterior to the adductor fossa, as well as along the dorso-lateral surface of the surangular and the dentary forming the mandibular shelf. The diffuse nature of a small posterior part of the insertion has been mentioned.

The medius portion is innervated by a posterolateral branch of the mandibular ramus of V piercing the muscle medially.

The *musculus adductor mandibulae externus profundus* (aep, Figs 11–12), deepest portion of the external adductor, lies against the lateral cranial wall laterally to the Gasserian ganglion and the maxillary ramus of the trigeminal nerve, posterolaterally to the pseudotemporalis muscle, and medially to the superficial and medius portions of the external adductor.

Extending anteroventrally, the profundus portion arises fleshily behind the postfrontal, on the lateral surfaces of the parietal downgrowth and the anterior superior process of the pro-otic (Fig. 11), as well as anterolaterally on the pro-otic proper (Fig. 12). The area of origin is bounded dorsally by the dorsolateral ridge of the parietal.

This muscle has no direct contact with the lower jaw and inserts fleshily along the entire medial surface of the vertical lamina, and along the dorsal half of the upper surface of the medial lamina of the bodenaponeurosis (Fig. 11). Dorsally to the vertical lamina of the bodenaponeurosis no partition exists between the superficial and profundus muscles (although the latter remains discrete owing to the oblique orientation of its fibres, as opposed to the near vertical orientation of the superficial fibres) (Fig. 11), whereas posterior to the bodenaponeurosis no distinction is apparent between the profundus and medius muscles (Fig. 12). However, the extent of each portion may be fairly easily determined.

The profundus portion is innervated by a branch leaving the mandibular ramus of V immediately below the Gasserian ganglion and turning dorsally for a short distance to enter the muscle medially.

Musculus adductor mandibulae posterior

The posterior division of the adductor mandibulae group is present as a single muscle, the *musculus adductor mandibulae posterior* (ap, Figs 11–13). It extends anteroventrally from the quadrate to the mandible and lies laterally to the mandibular ramus of the trigeminal nerve and medially to the extracolumella (Fig. 12). It is straddled over its entire length by the medius portion of the external adductor, although separated from it by the lateral and medial laminae of the quadrate tendon (Fig. 11).

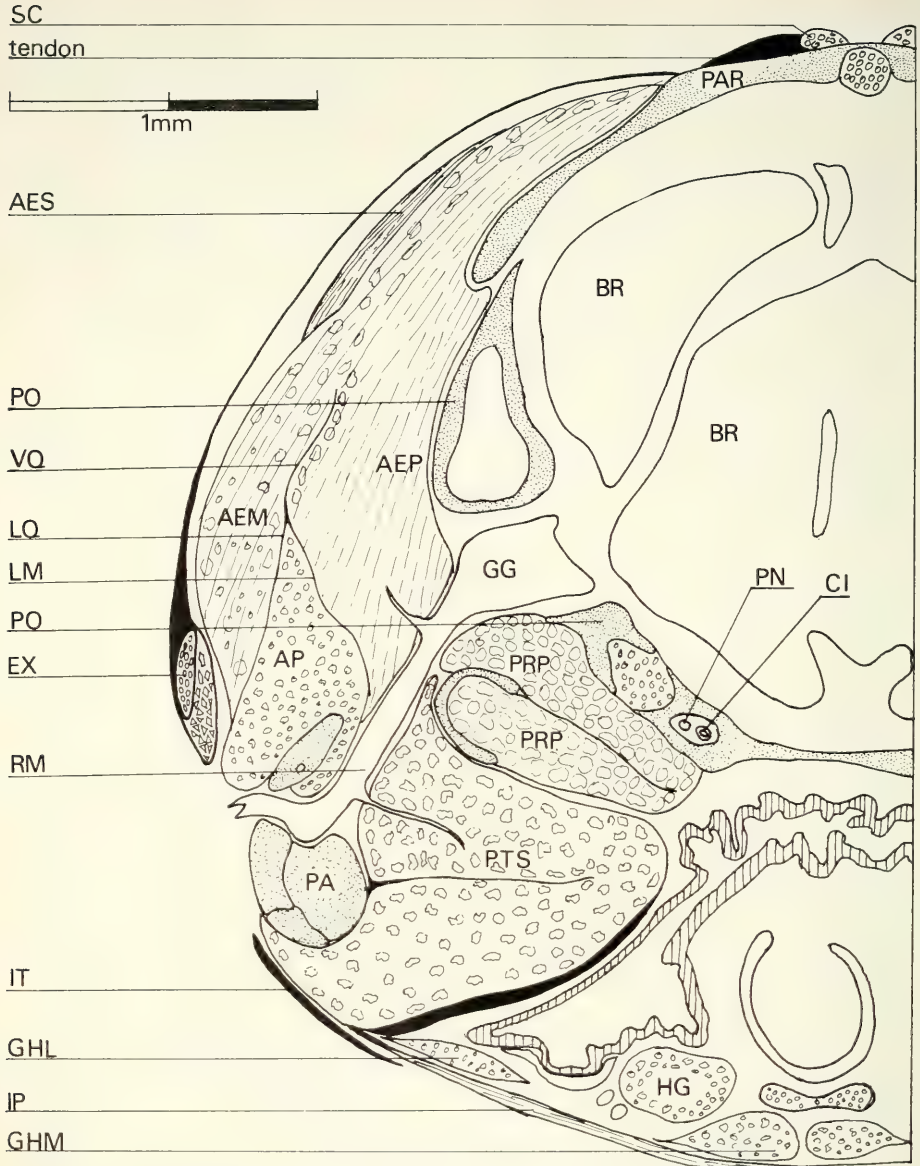


Fig. 12. Cross-section of the skull at the level of the mandibular ramus of V.

The muscle arises fleshily from the slightly concave medial surface of the quadrate, dorsomedially to and in line with the jaw articulation, as well as dorsally to the posterior extremity of the protractor pterygoideus muscle and the attachment of the quadrate ramus of the pterygoid (Fig. 13). The origin is also ventrolateral to the pro-otic and anterior to the stapes, with a few of the

most dorsal fibres arising dorsally to the stapes (Fig. 14). Fibres also arise from the anterior border of the quadrate. The quadrate tendon covers the posterior adductor completely (Fig. 12) except at the anterior extremity of the muscle in the region of the anterior supra-angular foramen where, over a short distance, the fibres of the posterior adductor are continuous with those of the medius portion of the external adductor. However, apart from obscuring the exact anterior border of the insertion, this is of little importance since the muscles are effectively separated, in practice, by the quadrate tendon. In addition, some of the posterior adductor fibres arise from the inferior surfaces of the lateral and medial laminae of the quadrate tendon.

The muscle inserts fleshily on to the mandible in an area extending from the articular facet to the base of the coronoid process. Its posterior extremity is pierced ventromedially by a small, robust tendon (Fig. 13), receiving the

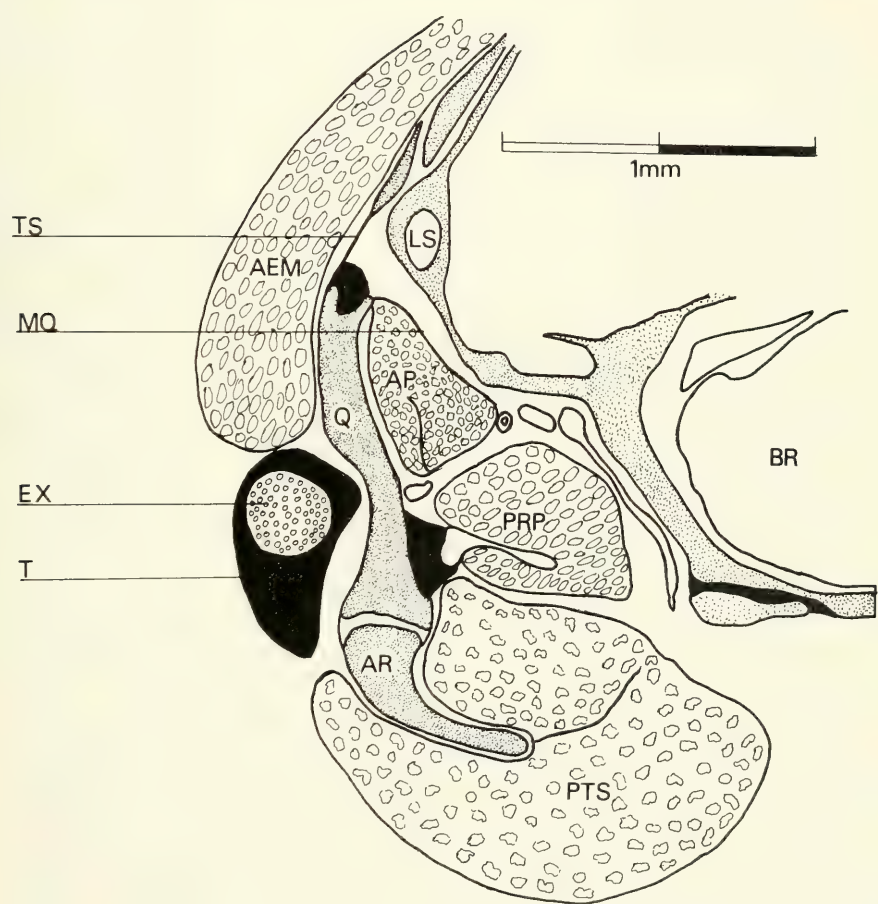


Fig. 13. Cross-section of the skull at the level of the quadrate.

insertion of the fibres arising in line with the jaw articulation on the medial surface of the quadrate. This tendon extends anteriorly for a short distance to attach immediately anterior to the articular facet on the dorsomedial surface of the articular process. The rest of the fibres straddle the mandible and insert dorsomedially on the surangular, within and around the adductor fossa (Fig. 11) on that part of the prearticular forming the ventral rim of the adductor fossa, and anterior to the fossa on the dorsomedial surface of the prearticular. A few fibres attach dorsomedially to the posterior process of the coronoid. In addition, fibres of this part of the muscle also insert on a small, vertical tendon running dorsally along the surangular ridge and situated within the muscle itself (Fig. 11). The tendon extends from the anterior border of the muscle to a point in line with the anterior border of the mandibular ramus of V, and fibres insert along its lateral and medial surfaces. The lateral fibres of the muscle insert on the mandibular shelf (Fig. 11), attaching dorsolaterally on to the surangular and dentary from the articular facet to near the base of the coronoid process.

A posterolateral branch of the mandibular ramus of V ramifies within the medius portion of the external adductor, with one branch piercing the medial lamina of the quadrate tendon to innervate the posterior adductor.

Musculus adductor mandibulae internus

According to Lakjer (1926) the third main division of the adductor mandibulae group, the internal adductor musculature, consists of two separate muscles, the m. pseudotemporalis and m. pterygoideus. Both muscles are present in *Typhlosaurus aurantiacus* as well-defined groups of fibres situated at right angles to one another.

The musculus adductor mandibulae internus pseudotemporalis (p, Figs 9–11) is a single, dorsoventral group of fibres located anteriorly within the temporal indentation, and although the bulk of its fibres are concentrated dorsomedially to the coronoid process, the muscle extends posteriorly to the anterior border of the mandibular ramus of V. As required by the classical definition it is situated medially to the maxillary, laterally to the ophthalmic and anteriorly to the mandibular rami of V. It lies medially to and against the superficial, anteromedially to the medius and anteriorly to the profundus portions of the external adductors; anteromedially to the posterior adductor muscle; laterally to the levator pterygoideus muscle and the epipterygoid bone, and anterolaterally to the pterygoideus muscle.

It arises fleshily from the anterolateral surfaces of the parietal downgrowth and the anterior superior process of the pro-otic, anterior to the origin of the profundus portion of the external adductor as well as from the lateral surface of the pro-otic membrane and the dorsal part of the epipterygoid bone.

The muscle inserts on the medial surface of the coronoid bone, utilizing the medial coronoid groove which extends from the apex of the coronoid process to the medial surface of the posterior process of the coronoid bone (Fig. 10). A small tendon attaching to the coronoid bone extends along the

lower rim of the medial coronoid groove and underlies the pseudotemporalis muscle, receiving the insertion of its medial fibres (Fig. 9). Behind the coronoid bone a few fibres insert on to the medial surface of the prearticular bone (Fig. 11).

The muscle is innervated by a branch of the mandibular ramus of V which leaves the anterior border of the ramus directly below the Gasserian ganglion and courses anteriorly for a short distance to enter the muscle posterodorsally.

The *musculus adductor mandibulae internus pterygoideus* (pts), is the largest single muscle in the head of *Typhlosaurus aurantiacus* and extends from the infra-orbital fenestra to the posterior extremity of the mandible. It has a small head which expands posteriorly to form a large rounded masticatory cushion, appropriately termed 'Kauwulst' by Lakjer (1926). The 'Kauwulst' is the most prominent part of the muscle and, with its opposite number, limits the aperture of the throat. It lies deep to the intermandibularis posterior muscle and the mandibulo-hyoid musculature, medially to the insertional tendon of the cervicomandibularis muscle and laterally to the protractor pterygoidei muscle and the pterygoid bone.

The muscle arises mainly from the outer surface of the pterygoid bone (Fig. 9) and from the inner surface of an extensive tendon originating lateral to the infra-orbital fenestra. Anteriorly the muscle is divided into two short slips, one arising dorsally from both the posterolateral surface of the palatine and the anterolateral border of the pterygoid and the second one arising ventrally on the posterolateral border of the palatine and the anterolateral surface of the pterygoid. The two muscle slips become confluent at a point in line with the anterior border of the levator pterygoideus muscle.

Some fibres arise fleshily along the outer lateral and ventral surface of the gutter-shaped pterygoid bone (Fig. 11). The major part of the origin, however, is from the exceptionally strong tendon arising lateral to the infra-orbital fenestra on the ventral surface of the palatal complex. The tendon arises behind the ventrolateral process of the maxillary on the ventral surface of the ectopterygoid, the posteroventral surface of the palatine and on the ventral surface of the pterygoid in front of the basipterygoid recess. Anteriorly the tendon covers the origin of the ventral slip of muscle and forms a thick pad medial to the angle of the mouth (Fig. 9). The pad presumably protects the fibres from damage by deflecting the coronoid process laterally during adduction of the jaw. Posteriorly the tendon broadens to cover the anterior two-thirds of the ventral surface of the muscle. Most of the fibres of the pterygoideus muscle arise from the inner surface of this tendon.

The muscle inserts on the retroarticular process of the mandible (Fig. 13). In front of the process the ventral border of the mandible is concave to accommodate the lateral fibres of the muscle which wrap around the jaw behind the posteroventral extremity of the dentary. The muscle envelops the retroarticular process, with fibres inserting on to its medial, ventral and lateral surfaces. Medial to the jaw a ribbon-like tendon lies within the muscle and attaches

ventrally to the retro-articular process (Fig. 13). Its dorsal and ventral surfaces are utilized for insertion.

The muscle is innervated by a branch of V which leaves the mandibular ramus medially, in line with the posterior supra-angular foramen, to pierce the muscle laterally.

Intermandibular musculature

The intermandibular muscles, innervated by V, form part of the trigeminal musculature. Situated anteroventrally to the constrictor colli, their fibres extend transversely between the rami of the lower jaws as thin superficial sheets of muscle, deep only to the skin and to the insertional tendon of the cervico-mandibularis muscle. Two portions, an anterior and a posterior, are present.

The m. intermandibularis anterior (ia, Figs 9–10), four to six fibres in thickness, lies anteriorly between the rami of the lower jaws. It is laterally interrupted at right angles by bundles of the geniohyoideus muscle which insert anteroventrally on the jaw. According to Camp (1923) these interdigitations (of which there are five in *Typhlosaurus aurantiacus*) are always present in lizards. The muscle lies superficially to the geniohyoideus and genioglossus muscles and can be divided into a more posteriorly lying superficial portion and a more anteriorly lying profundus portion.

The superficial portion arises medially on the jaw (Fig. 10) between the posterior mylohyoid foramen and the combined foramen for the anterior mylohyoid and the infra-alveolar nerves, along the medial surface of the pre-articular, splenial and dentary bones. It inserts anteriorly along the ventral midline onto the sheet of fascia receiving the insertion of the constrictor colli muscle. Three bundles of geniohyoideus fibres interdigitate with the superficial portion of the intermandibularis anterior muscle.

The profundus portion of the m. intermandibularis anterior lies immediately anterior to the superficial portion, posteriorly overlain by the latter. It arises medially to the jaw from the dorsolateral surface of the sublingual gland and the outer surface of the buccal lining, dorsal to the gland. The origin extends from a point in line with the anterior mylohyoid and the infra-alveolar foramen to just behind the jaw symphysis. The muscle inserts tendinously in the ventral midline anterior to the superficial portion of the intermandibularis anterior muscle. Two bundles of the geniohyoideus fibres interdigitate with the profundus portion.

The intermandibularis anterior is innervated by a branch of the posterior mylohyoid nerve, which enters the superficial portion posteriorly, and by a branch of the anterior mylohyoid nerve, which enters the profundus portion superficially.

The m. intermandibularis posterior (ip, Fig. 12), two fibres in thickness, lies immediately behind the intermandibularis anterior. The two muscles are separated by the most posterior interdigitation between the geniohyoideus and intermandibularis anterior muscles. The intermandibularis posterior does

not interdigitate with the geniohyoideus muscle and is well separated from the constrictor colli. It covers the throat ventrally, lateral to the midline, and lies superficially to the hyoglossus, the genioglossus and the geniohyoideus muscles, the masticatory cushion (Kauwulst) of the pterygoideus muscle and the hypoglossal nerve (Fig. 12).

The m. intermandibularis posterior arises tendinously from a thin sheet of fascia which covers the pterygoideus muscle laterally (Fig. 12) and attaches to the lateral surfaces of the surangular and dentary bones between the jaw articulation and the posterior mylohyoid foramen. The muscle inserts tendinously in the ventral midline on to the same sheet of fascia which receives the insertion of the constrictor colli muscle and the intermandibularis anterior muscle (Fig. 12).

It is innervated by a branch of the posterior mylohyoid nerve, entering the muscle superficially via the posterior mylohyoid foramen.

Tongue musculature

In *Typhlosaurus aurantiacus* the tongue is of the usual scincid type, bluntly triangular with a bifurcate apex and posteriorly divided into two roots situated lateral to the glottis. Behind the apex its dorsal surface is covered with scale-like papillae, on which glandular surfaces are restricted to the basal portions. According to Camp (1923) the position of the glandular surfaces is a diagnostic feature of the Scincomorpha.

The tongue is composed of fibres of both extrinsic and intrinsic musculature. The intrinsic fibres control the shape of the tongue, while motion is controlled by the extrinsic fibres. Sondhi (1958) found that in some Indian reptiles the apparently distinct groups of intrinsic fibres are actually parts of the hyoglossus muscle and do not deserve independent status. In *Typhlosaurus aurantiacus* these fibre groups are equally distinct and in view of the marked differences between their orientation and that of the hyoglossus muscle, they will be described separately.

Extrinsic muscles

The m. hyoglossus (hg, Figs 9–12) is a paired longitudinal muscle, extending parallel to the midline from the hyoid apparatus to the anterior tip of the tongue. Posteriorly the muscle is dorsoventrally flattened and lies ventrolaterally to the trachea and the oesophagus, laterally to the first ceratobranchial and dorso-laterally to the posterior part of the geniohyoideus muscle. Anteriorly it becomes cylindrical, turning dorsally to the undersurface of the tongue to lie laterally to the lingual process of the hyoid, medially to the geniohyoideus muscle, and ventrolaterally to the glottis. It is sheathed by fibres of the vertical intrinsic musculature. The most anterior part of the muscle lies dorsomedially to the genioglossus muscle, and tapers towards the jaw symphysis to terminate ventrally to the anterior tip of the tongue.

The muscle arises superficially in the throat region from the anterior surface of the first ceratobranchial, medially to the origin of the geniohyoideus lateralis muscle, ventrolaterally to the oesophagus and dorsolaterally to the origin of the geniohyoideus medialis muscle. It inserts fleshily along the ventral surface of the tongue, between the medial and lateral vertical fibres of the intrinsic musculature and medially to the insertion of the genioglossus muscle. The muscle is innervated by a branch of the hypoglossal nerve.

The *m. genioglossus* (ggl, Figs 9–12) is a paired muscle, lying laterally to the ventral midline and extending from the jaw symphysis to the posterior border of the tongue. In front it lies dorsolaterally to the geniohyoideus medialis muscle, ventrolaterally to the hyoglossus muscle, and medially to the sublingual gland. At the back the muscle extends laterally around the ventral surface of the sublingual gland and behind it the fibres lie ventrally to the lateral margin of the oral membrane. A small cylindrical group of fibres separates antero-ventrally from the genioglossus muscle and extends posteriorly, lying ventro-medially to the genioglossus muscle and dorsally to the geniohyoideus medialis muscle. In line with the glottis the fibres of this bundle become confluent with those of the geniohyoideus medialis muscle. It is innervated by a minute ramus branching from the hypoglossal nerve.

The genioglossus arises tendinously at the jaw symphysis, taking origin from the inner ventral surface of the dentary immediately lateral to the symphysis, from the connective tissue surrounding the symphysis and, in the midline, from the sheet of fascia covering the throat musculature ventrally. It inserts along the ventral surface of the tongue, laterally to the hyoglossus muscle and the lateral group of vertical intrinsic fibres, and interlaces with the transverse fibres of the intrinsic musculature. The muscle is innervated by a branch of the hypoglossal nerve.

Intrinsic musculature

The intrinsic muscles are innervated by the hypoglossal nerve and consist of three groups of fibres, i.e. the vertical lingual, the longitudinal lingual and the transverse lingual fibres, and although they interweave to some extent each group remains distinct.

The *m. verticalis linguae* (vl, Figs 9–11) consists of a superior and an inferior group of fibres. The superior fibres lie dorsally to the transverse lingual muscle and form the papillae of the tongue. The inferior fibres lie ventrally to the transverse lingual muscle, interlace with its fibres, and extend from the apex of the tongue to the glottis. These fibres consist of a medial and a lateral group. The lateral group lies between the genioglossus and the hyoglossus muscles while the medial group lies between the hyoglossus muscle and the midline. The two groups meet tendinously ventral to the hyoglossus muscle.

The *m. transversalis linguae* (tl, Figs 9–11) lies between the inferior and superior vertical fibres. Its fibres extend across the width of the tongue from the apex to the roots and interlace with the fibres of the inferior vertical, the

hyoglossus and the genioglossus muscles.

The m. longitudinalis linguae (ll, Figs 9–10) lies ventrally along the rim of the tongue, laterally to the insertion of the genioglossus muscle on either side. It extends from behind the apex of the tongue to nearly in line with the glottis as a single cylindrical bundle of fibres, breaking up into smaller bundles posteriorly and becoming obscured by the insertion of the genioglossus muscle.

The m. geniohyoideus lateralis (ghl, Fig. 12) is a narrow muscle extending between the ventral surface of the jaw and the hyoid apparatus. It lies ventromedially to the jaw, ventrolaterally to the genioglossus muscle, deep to the intermandibularis posterior muscle, and ventrally to the 'Kauwulst' of the pterygoideus muscle.

It arises fleshily on the ventral surface of the jaw from a short distance behind the symphysis to the posterior mylohyoid foramen. The origin consists of five successive bundles of longitudinal fibres interlacing with the fibres of the intermandibularis anterior muscle. The muscle inserts on the anterolateral tip of the sole remaining posterior prong of the hyoid apparatus (usually taken to be the first ceratobranchial). The insertion is fleshy and lies lateral to that of the geniohyoideus medialis and hyoglossus muscles. The muscle is innervated by a branch of the glossopharyngeal nerve.

The m. geniohyoideus medialis (ghm, Figs 9–12) is a superficial group of fibres extending from the anteroventral surface of the genioglossus muscle to the hyoid apparatus. The muscle lies laterally to the ventral midline, deep to the intermandibularis musculature, ventromedially to the genioglossus muscle and below the bundle of fibres extending between it and the genioglossus muscle. Posteriorly the muscle is flattened dorsoventrally and lies ventromedially to the hyoglossus muscle, deep to the intermandibularis posterior muscle and medially to the hypoglossal nerve. Anteriorly the muscle becomes triangular in cross section and lies deep to the intermandibularis anterior muscle.

The muscle arises tendinously behind the origin of the genioglossus muscle, from the deep surface of the sheet of fascia covering the throat musculature ventrally and inserts fleshily along the ventral surface of the first ceratobranchial, ventromedially to the origin of the hyoglossus muscle. The muscle is innervated by a branch of the glossopharyngeal nerve.

Depressor mandibulae group

The m. depressor mandibulae (Figs 14–16) is a superficial sheet of fibres behind the adductor musculature. It lies laterally to the stapedial artery, the lateral head vein and the hyomandibular ramus of VII. On its ventrolateral surface it is obliquely overlain by the prominent cervicomandibularis muscle which in its turn is covered by the dorsoventral fibres of the sheet-like constrictor colli muscle. There is no indication in either *Typhlosaurus aurantiacus* or *Acontias meleagris* that the depressor mandibulae and cervicomandibularis muscles are continuous.

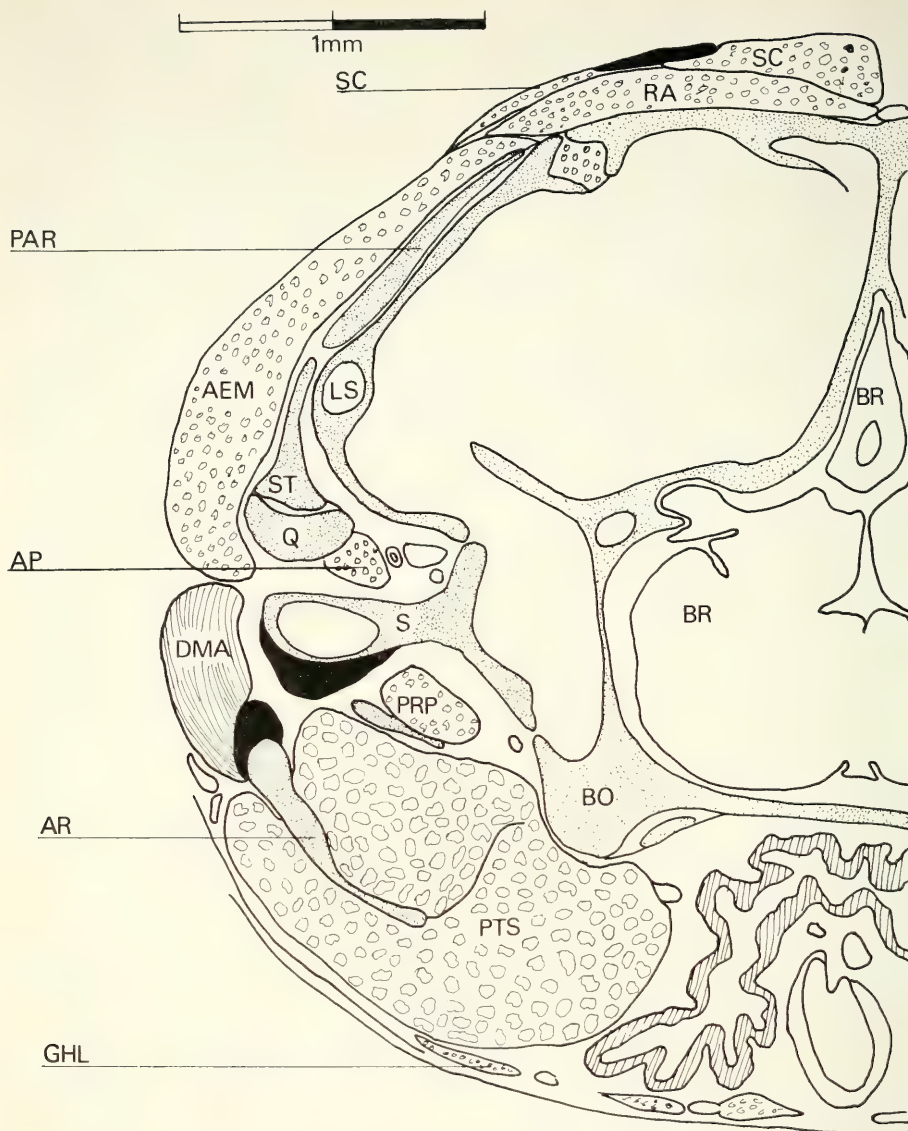


Fig. 14. Cross-section of the skull at the level of the stapes.

The depressor mandibulae consists of an anterior portion arising cranially and a posterior portion arising cervically. The anterior portion (dma, Figs 7, 14–15) is spindle-shaped and lies immediately behind the stapes. It arises fleshily from the anterolateral surface of the fused exoccipital-opisthotic bone, posterodorsally to the quadrate head, and extends vertically downwards, laterally to the posterior half of the stapedia footplate, to insert fleshily on the dorsal

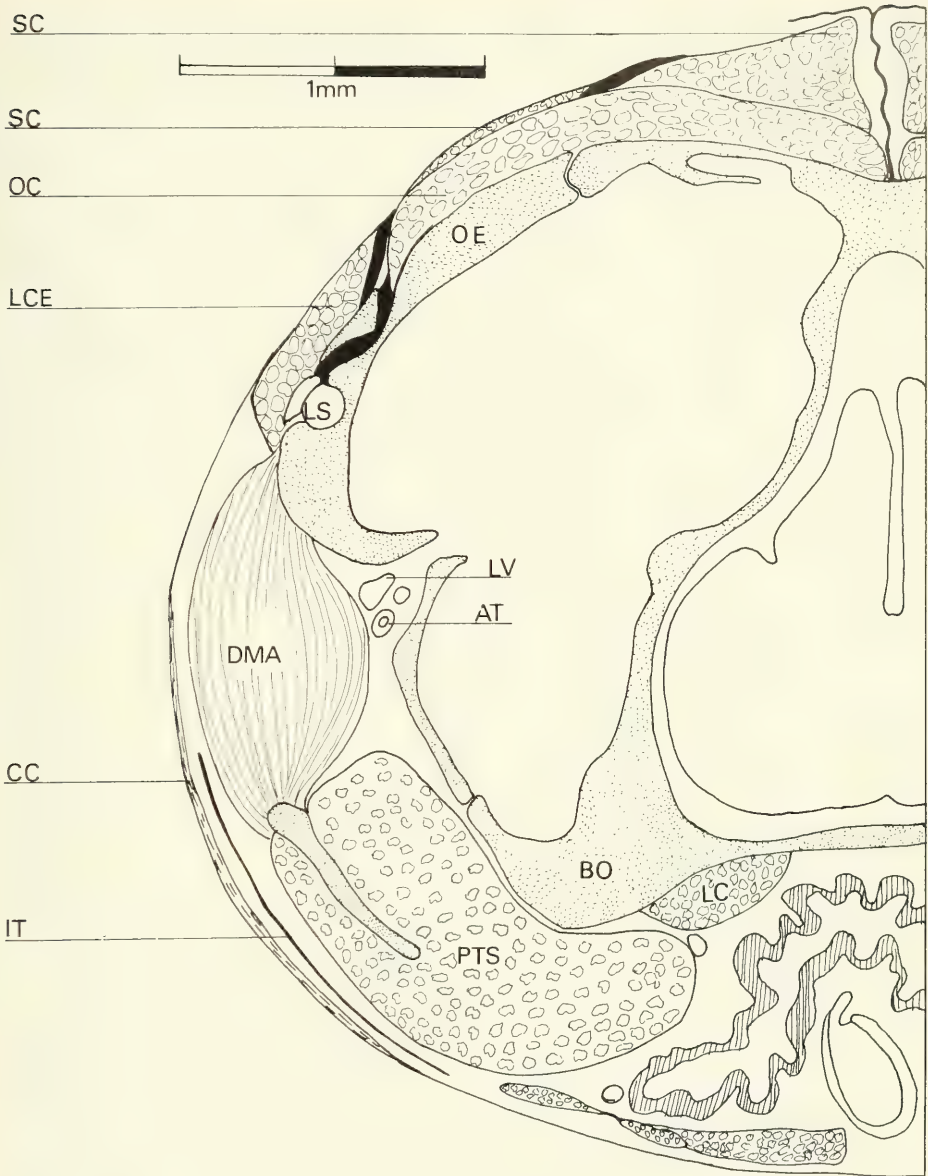


Fig. 15. Cross-section of the skull at the level of the anterior portion of the depressor mandibulae.

surface of the retro-articular process behind the tendon connecting the stapes to the mandible.

The posterior portion (dmp, Fig. 16), a thin triangular sheet of fibres lateral to the obliquus capitis magnus muscle and the innervations of the longis-

simus and episternocleidomastoideus muscles, lies against the posterior border of the cranial portion of the depressor mandibulae. It arises along the insertional tendon of the longissimus cervicis muscle, ventrolateral to the spinalis capitis

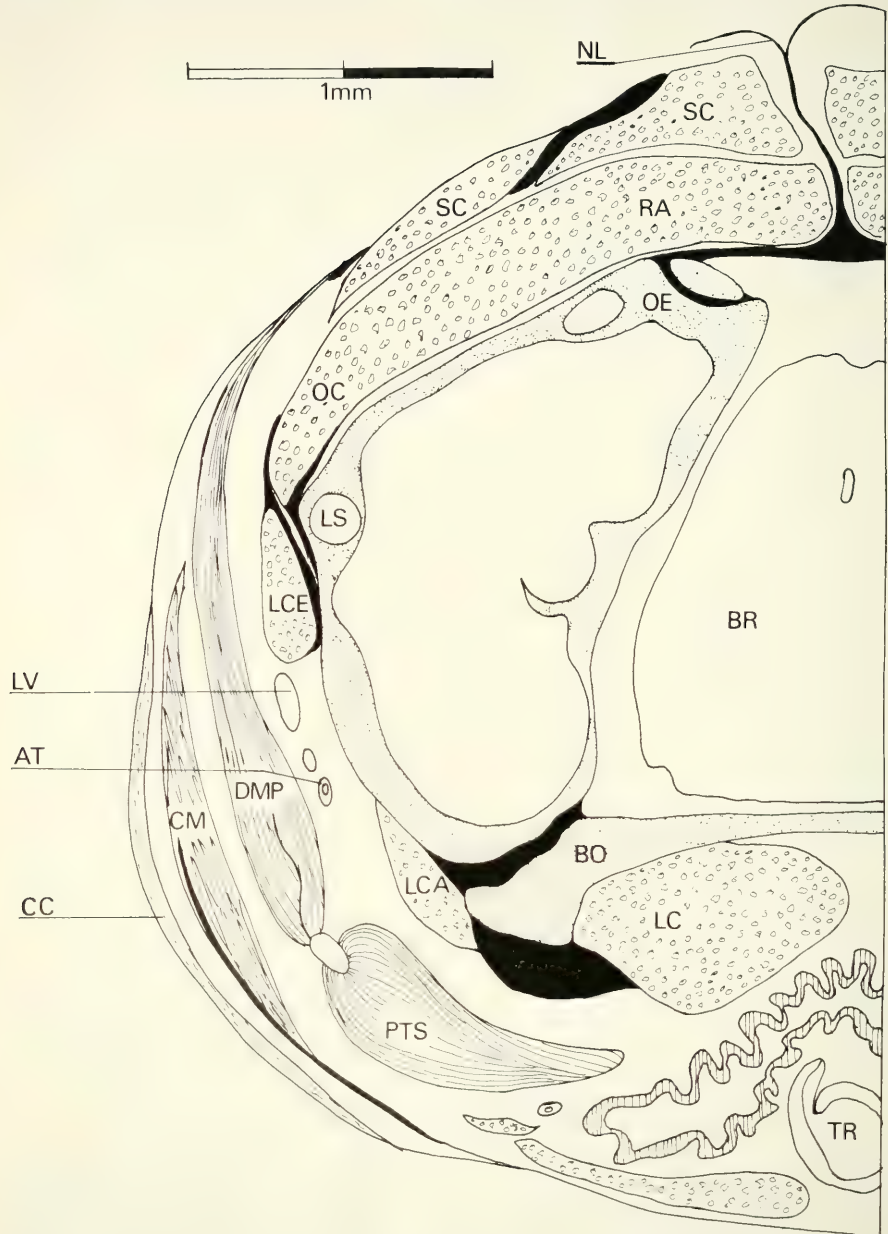


Fig. 16. Cross-section of the skull at the level of the posterior portion of the depressor mandibulae.

muscle and between the origin of the cervicomandibularis muscle and the posterodorsal border of the adductor mandibulae musculature. The fibres converge anteroventrally to insert behind those of the cranial portion by means of a small tendon on to the posterodorsal extremity of the retro-articular process of the mandible.

The depressor mandibulae is innervated by the hyoid ramus of VII, which branches off behind the stapedial footplate from the hyomandibular ramus, pierces the medial surface of the muscle and courses anteriorly for a short distance within it.

The m. cervicomandibularis (cm, Figs 6–7, 16) is a large elongated sheet of fibres medial to the constrictor colli muscle. It extends antero-ventrally, superficial to the cervical musculature, from the level of the seventh dorsal vertebra to the anteroventral surface of the jaw. It lies lateral to the episternocleidomastoideus muscle, the longissimus cervicis and capitis muscles, and the anterior parts of the iliocostalis system and the oblique hypaxial muscles.

The muscle arises fleshily from the anterolateral surface of the iliocostalis system and the oblique hypaxial muscles, from the longissimus cervicis muscle, and along its border from the dorsal intermuscular septum. Its fibres extend forward only as far as the posterolateral surface of the 'Kauwulst' of the pterygoideus muscle where they attach to a thin sheet of fascia which covers the 'Kauwulst' laterally and ventrally and lies superficial to the throat muscles. Anteriorly the tendon becomes aponeurotic and inserts along the ventral surface of the jaw, from the anterior border of the posterior intermandibular muscle to just lateral to the symphysis.

The m. cervicomandibularis is innervated by a branch of VII which pierces the medial surface of the muscle in line with the occipital condyle of the skull.

The m. constrictor colli (cc, Figs 5, 15–16) is a thin superficial sheet of fibres covering the cervical region immediately below the skin. Its fibres extend anteroventrally from the cervical region to cover the pterygoideus muscle posterolaterally and the cervicomandibularis muscle anteroventrally. The muscle is triangular in lateral aspect and its anterior border lies immediately behind the extracolumella. The upper border of the muscle tapers postero-ventrally and it terminates at a point ventrolateral to and approximately in line with the third vertebra.

The muscle arises fleshily from a thin superficial sheet of cervical fascia extending ventrally from the dorsal intermuscular septum, situated between the transversospinalis and longissimus systems, to insert ventrolaterally in the cervical region on to a superficial sheet of fascia covering the throat from the jaw symphysis posteriorly to the rectus abdominis muscles.

The muscle is innervated by a branch of the hyomandibular ramus of VII which passes through the cervicomandibularis muscle to enter the deep surface of the constrictor colli in line with the posterior border of the condyle of the skull.

Cervical musculature

In contrast to non-fossorial lizards, the cervical extensor and flexor muscles in *Typhlosaurus aurantiacus* play an active role during locomotion and especially during burrowing movements. However, in spite of this added function the distribution of the individual muscles retains a pattern common to saurians in general.

The nuchal ligament is a vertical mid-dorsal sheet in the cervical region extending from the occiput to the neural spine of the axis. Dorsally the ligament is continuous with the fascia covering the transversospinalis system. This fascia is laterally continuous with the dorsal intermuscular septum lying between the transversospinalis and longissimus systems.

The m. spinalis capitis (sc, Figs 6, 12, 14–16) is a flat, dorsally situated muscle extending immediately below the skin from the level of the twelfth vertebra to the occiput. It lies lateral to the nuchal ligament and dorso-medial to the anterior part of the longissimus dorsi muscle and its cervical derivative, the longissimus cervicis. The muscle covers the rectus capitis anterior and obliquus capitis magnus muscles. The lateral fibres arise fleshily from the lateral margin of the dorsal intermuscular system.

The fibres insert tendinously on to the posterodorsal surface of the parietal bone. The insertion is confined to a shallow depression on the parietal anterior to the supra-occipital-parietal suture and lateral to the small mid-dorsal ridge formed by the ascending process of the tectum synoticum.

The muscle is innervated by a branch of the dorsal ramus of the first spinal nerve which passes between the rectus capitis posterior and the obliquus capitis magnus muscles.

The m. rectus capitis posterior and the m. obliquus capitis magnus are partially fused and appear as a single group of fibres. However, in the interests of clarity they will be described separately.

The m. rectus capitis posterior (rp, Figs 6, 8) extends from the atlas to the occiput. It lies ventral to the spinalis capitis muscle, lateral to the nuchal ligament, dorso-medial to the longissimus cervicis muscle and antero-medial to the obliquus capitis magnus muscle, which arises posterior to it. In *Typhlosaurus aurantiacus* the rectus capitis posterior is a single muscle and it probably represents the fused rectus capitis superficialis and profundus muscles still present, although partially fused, in such forms as *Iguana iguana* (Olson 1936). The rectus capitis posterior muscle can be distinguished from the obliquus capitis magnus muscle by the passage of the dorsal ramus of the first spinal nerve between them as in *Ctenosaura pectinata* (Oelrich 1956).

The muscle arises fleshily from the lateral surface of the axial neural arch and the aponeurotic fascia covering the atlanto-occipital gap. Some fibres also arise from the dorsal surface of the obliquus capitis magnus muscle.

The fibres insert fleshily, deep to the spinalis capitis muscle and dorso-medial to the insertion of the obliquus capitis magnus muscle, on to the dorsal surface of the supraoccipital bone and that part of the fused exoccipital-

opisthotic bone dorsal to the ridge formed by the lateral semicircular canal of the internal ear.

The muscle is innervated by a branch of the dorsal ramus of the first spinal nerve.

The *m. obliquus capitis magnus* (oc, Figs 6, 8) extends from the fifth vertebra to the lateral margin of the fused exoccipital-opisthotic bone. It lies ventral to the *spinalis capitis* muscle, posterolateral to the *rectus capitis posterior* muscle, dorsal to the anterior part of the *spinalis dorsi* muscle, dorsal to the *rectus capitis anterior* muscle and medial to the *longissimus cervicis* muscle.

It arises fleshily from the dorsal extremities of the neural spines of the third, fourth and fifth vertebrae, the tendinous tissue connecting the spines and from the fascia covering the *spinalis dorsi* muscle.

The fibres extend obliquely forward and insert tendinously on to the lateral margin of the fused exoccipital-opisthotic bone, attaching to the ridge formed by the lateral semicircular canal of the internal ear, ventrolateral to the *rectus capitis posterior* muscle and dorsomedial to the insertion of the *longissimus cervicis* muscle.

The muscle is innervated by the dorsal ramus of the first spinal nerve.

The *m. longissimus dorsi* lies ventrolateral to the *transversospinalis* system and dorsal to the heads of the ribs. At the level of the fourth vertebra it divides into a dorsal and a ventral group of fibres. The dorsal group, the *m. longissimus cervicis* (lce, Figs 6–8) lies ventrolateral to the *spinalis capitis* and *rectus capitis posterior* muscles and lateral to the *obliquus capitis magnus* muscle. The muscle arises fleshily approximately from the level of the seventh to the second vertebrae from the fibres of the *longissimus dorsi* muscle. It extends anteriorly dorsal to the *longissimus capitis* muscle and lateral to the *obliquus capitis magnus* muscle, to insert tendinously on to the lateral margin of the fused exoccipital-opisthotic bone, lateral to the insertion of the *obliquus capitis magnus* muscle and medial to the insertion of the *episternocleidomastoideus* muscle.

The muscle is innervated by the dorsal ramus of the first spinal nerve.

The ventral group of fibres, the *m. longissimus capitis* (lca, Fig. 8), extends anteroventrally from the level of the fourth vertebra to the basal tuberosity of the basi-occipital bone. It lies ventral to the *longissimus cervicis* muscle, medial to the *episternocleidomastoideus* muscle, dorsolateral to the *longus colli* muscle and lateral to the *rectus capitis anterior* muscle. The fibres arise fleshily from the *longissimus dorsi* muscle and the synapophysis of the first four vertebrae to insert tendinously on to the basal tuberosity lateral to insertion of the *rectus capitis anterior* muscle and dorsomedial to the insertion of the *longus colli* muscle.

The muscle is innervated by a branch of the dorsal ramus of the first spinal nerve.

The *m. rectus capitis anterior* (ra, Fig. 8) is a group of short fibres extending from the axis to the occiput. The muscle lies ventrolateral to the axis, the

atlas and the occipital condyle of the skull; medial to the longissimus capitis muscle and dorsal to the anterior part of the longus colli muscle with which some of its ventral fibres are confluent.

It arises fleshily on the ventrolateral surface of the axis medial to the synapophysis and ventrolaterally on the atlas. The fibres insert fleshily on to the basioccipital and exoccipital-opisthotic bones. The insertion lies ventral to the insertion of the rectus capitis posterior muscle, dorsal to the insertion of the longus colli muscle and dorsomedial to the insertion of the longissimus capitis muscle.

The muscle is innervated by a branch of the first spinal nerve.

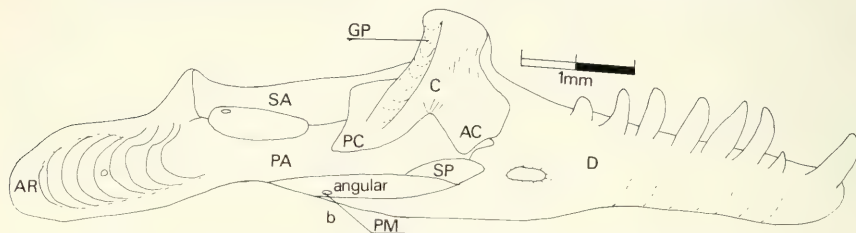


Fig. 17. Camera lucida drawing of the left lower jaw; lingual view.

DISCUSSION AND CONCLUSIONS

General

The morphology of fossorial skinks in general is paralleled by that of snakes in many ways and it is therefore interesting to note that according to the theory of Walls (1942) snakes originated as fossorial forms. Any evaluation of the musculature of *Typhlosaurus aurantiacus* must be made in the light of the fact that the animal leads a predominantly subterranean existence which does not involve the construction of burrows. Huey *et al.* (1974) describes *Typhlosaurus* as a sand swimming lizard which normally moves in a lateral sinuous path beneath the sand. *T. aurantiacus* has a subterminal mouth as in other fossorial lizards, e.g. *Acontias*. The position of the mouth prevents soil particles from entering the buccal cavity during burrowing movements. De Weerd (1971) indicates that it is important to a fossorial lizard like *Dibamus* to use its mouth in a terminal position. This argument is based on the assumption that the lizard lives in a burrow and encounters its prey directly in front of it. Neither *Typhlosaurus* nor probably *Dibamus* lives in a burrow and consequently prey may be approached from any angle.

The animal uses its head as a burrowing tool, and the skull and its associated musculature are consequently strongly modified. Temporal arches and posttemporal fenestrae are absent. The elongated temporal region is strengthened by the lateral downgrowth of the parietal and the broad anterior superior processes of the pro-otic. These structures also serve as areas of origin to the

adductor musculature. The occipital region is strengthened by the fused exoccipital and opisthotic bones and the expanded nature of the occiput allows the cervical musculature to insert relatively far forward on to the skull.

As in *Dibamus* (Gasc 1968) *Typhlosaurus aurantiacus* lacks a m. levator bulbi. This condition is probably associated with the degeneration of the eyes. According to Haas (1973) the structural diversity of the m. levator bulbi in lizards appears not to be controlled by phylogenetic factors but rather by functional factors such as the presence or absence of a movable lower eyelid or a general reduction of the visual apparatus.

The m. pseudotemporalis is single in *Typhlosaurus aurantiacus* as in the Gekkonidae, the Pygopodidae and the snakes. De Weerd (1971) describes a single m. pseudotemporalis in *Dibamus* but fails to define the position of the muscle in relation to the maxillary ramus of V. It may well be that the muscle is in fact part of the m. adductor mandibularis externus. Gasc (1968) describes a m. pseudotemporalis in *Dibamus* consisting of two parts. Haas (1973) interprets Gasc's description as pertaining only to the posterior of the two portions. However, Gasc, on page 135, clearly states that: 'Une nappe profonde (fig. 9) formée par deux chefs. . . . Cette nappe pourrait correspondre, d'après ses insertions, aux deux chefs du m. adductor mandibularis medius (= pseudotemporalis); toutefois, la branche maxillaire du trijumeau passe ici au-dessous de ce plan musculaire.' From Gasc's figure 9 it is clear that the maxillary ramus of V lies medial to the m. pseudotemporalis. It is probable therefore that this muscle forms part of the m. adductor mandibularis externus and not the m. adductor mandibularis internus. According to Haas (1973) the gekkonids and pygopodids lack the m. pseudotemporalis superficialis but retain the profundus portion of the muscle which consists of an anterior and a posterior part. It is probable that the single muscle retained in *T. aurantiacus* represents the profundus portion of the m. pseudotemporalis and that the reduction of the m. pseudotemporalis in this animal is related to the loss of the temporal arches as Haas (1973) believes it to be in the case of gekkonids, pygopodids and snakes.

The depressor mandibulae is a relatively small muscle and (in theory) its position close to the fulcrum of the jaw is not functionally optimal. Since the opening of the jaw is usually assisted by gravity this condition is not a liability. However, in a lizard which feeds subterraneously the surrounding pressure of the soil may demand a more sophisticated arrangement of the jaw opening muscles. In *Typhlosaurus aurantiacus* the cervicomandibularis is probably the main jaw opening muscle since its origin on the neck musculature and ventral insertion on the jaw makes it ideally suited for this purpose. Camp (1923) notes that the cervicomandibularis muscle is enormously developed in all burrowers.

From the forwardly extended insertion of the cervical musculature on to the occiput and the lateral extension of the synapophyses of the axis and the three following vertebrae it is evident that this group of muscles plays an important role in locomotion. It serves to flex and extend the skull as well as

stiffen the atlanto-occipital joint during burrowing. The degree of fusion between individual cervical muscles seems logical in the light of their function.

Cranial kinesis

Versluys (1910, 1912) described the movable joints of the reptilian skull. He divided the skull into an 'occipital segment' consisting of the bones of the braincase and the parasphenoid, and a 'maxillary segment' comprising the rest of the skull. The intracranial movements between the two segments are known as kinesis and were interpreted by Versluys as a mechanism for increasing the gape of the mouth by lifting the snout. Various degrees of kineticism exist, and skulls ranging from akinetic, with little or no movement between the 'segments', to amphikinetic, in which more than two movable parts are found. The constrictor dorsalis group of muscles is responsible for the kinetic movements of the skull.

Versluys based his conclusions on morphological studies, but recent workers have made use of sophisticated methods to study live material. Frazetta (1962) who revised Versluys's terminology, used motion pictures to record the capture of prey as well as electrical stimulation and biomechanical analysis of the muscles. Iordansky (1970) used biomechanical analysis to extend the approach of Frazetta. In contrast to Versluys, Frazetta concluded that kinesis actually lessens oral gape. However, in spite of the advanced techniques employed by them, Frazetta and Iordansky are not in full agreement on certain aspects of kinesis.

It is evident that kinesis is a complex mechanism of which the functional significance is not yet fully explained. This is also clear from the variable nature of the constrictor dorsalis group of muscles in a form such as *Sphenodon*. Frazetta (1962) describes *Sphenodon* as akinetic whereas Ostrom (1962) describes a specimen which has both a levator pterygoidei and a protractor pterygoidei muscle. According to Ostrom, in previously described specimens of *Sphenodon* either one of these muscles were present but never both. The study of cranial kinesis therefore requires the application of sophisticated techniques to live specimens as well as the dissections of numerous examples of the same species. The scope of this paper and the paucity of material precludes an in-depth study of cranial kinesis in *Typhlosaurus aurantiacus* but, since the cranial muscles have been described in detail, a brief summary will be given here.

According to Bellairs (1969) fossorial lizards tend to become monokinetic or even akinetic. A reduction of intracranial movements seems logical in the light of strengthening the skull for burrowing. Usually it appears that the metakinetic bending plane between the supraoccipital and parietal bones is reduced in favour of the mesokinetic bending plane between the parietal and frontal bones as in *Acontias* (De Villiers 1939, Brock 1941, Van der Merwe 1944); *Monopeltis capensis* (Kritzing 1946); *Anniella* (Toerien 1950, Bellairs 1969); *Nessia* (Bellairs 1969) and *Dibamus* (De Weerd 1971). According to Leonard (1973) the less specialized burrowing skink *Scelotes* is amphikinetic.

In *Typhlosaurus* the presence of a small levator pterygoidei muscle, a substantial protractor pterygoidei muscle, a synovial articulation between the quadrate and the skull and a movable basipterygoid articulation clearly indicate a certain amount of intracranial movement. Because of the posterior expansion of the skull, the occipital bones have become fused and the insertional areas of the cervical musculature have increased to such an extent that the spinalis capitis muscle inserts dorsally on the posterior part of the parietal, anterior to the position of the metakinetic bending plane.

The position of this muscle suggests a sharp reduction, if not total absence, of a functional metakinetic bending plane, despite the presence of the cartilaginous ascending process of the tectum synoticum. The post-orbital bar is incomplete and according to Leonard (1973) this is a prerequisite for mesokinesis. Smit (1964) agrees that metakinesis is reduced or absent and states that movement is clearly possible between the parietal and the frontal bones, indicating that the *Typhlosaurus* skull is definitely mesokinetic.

Jaw mechanics

According to Ostrom (1964) the vertebrate lower jaw operates as a lever of the third class during adduction. This arrangement ensures maximum depression of the jaws with a minimum length of adductor muscle fibres. In a system of this kind the mechanical advantage is directly proportional to the length of the moment arm if the applied force (adductor musculature) remains constant. The moment arm is defined as the perpendicular distance between the line of applied force and the fulcrum (Fig. 18A). In the jaw the moment arm represents the distance between the jaw articulation and the tip of the coronoid process.

If the line of applied force functions in a posterior direction, at an angle of less than ninety degrees to the long axis of the lever, the moment arm FB (Fig. 18A) is no longer perpendicular to the applied force and is effectively displaced to position FB' (Fig. 18B) with the result that the length of the moment arm is decreased and the system functions at a disadvantage. However, this condition can be overcome by raising the point of attachment (development of a coronoid process) of the applied force (Fig. 18C).

From Figure 18C it follows that: $m^2 = x^2 + y^2$.

The moment arm (m) is therefore a function of x (the distance between the coronoid process and the jaw articulation) and y (the height of the coronoid process). If y is constant x will determine the line of muscle action (θ) and vice

versa, because $\tan \theta = \frac{y}{x}$.

Consequently, with y constant any decrease in x will result in a more posteriorly directed line of muscle action, or, alternatively, an increase in x will result in a more perpendicular orientation of the adductor fibres. If x is kept constant and y decreased the fibre orientation would become more vertical

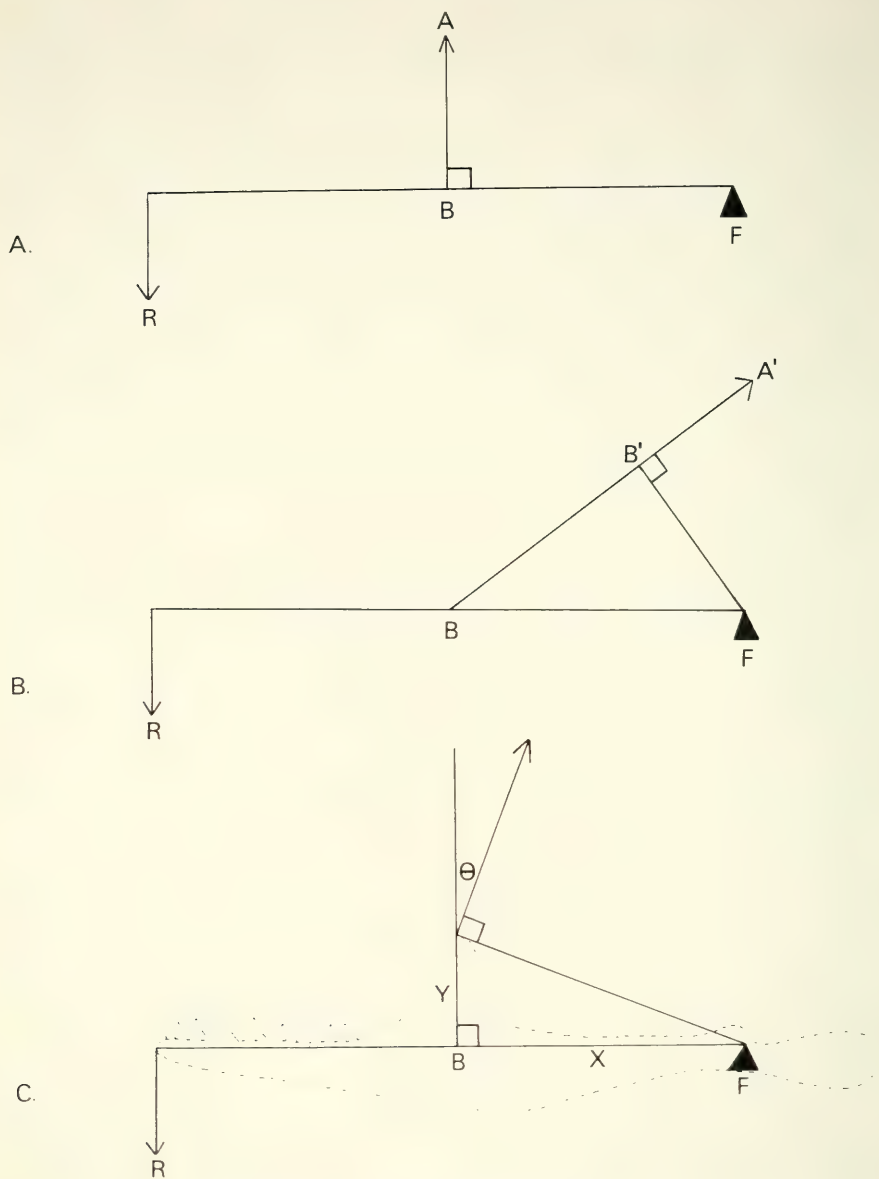


Fig. 18. Diagram to illustrate the action of the lower jaw.

and if y is increased the fibre orientation would become more posteriorly directed. It is clear therefore that the coronoid process in terms of height (y) and distance from the articulation (x) is functionally important in determining the action of the lower jaws and its associated musculature, and not as De Weerd (1971) suggests, mainly a strengthening device.

The vertebrate lower jaw, seen in terms of the mechanics of a third class lever, would theoretically function at optimal efficiency with the adductor fibres orientated perpendicular to the long axis of the lower jaw and inserted on to the jaw as close as possible to the symphysis.

Ostrom (1964) notes two disadvantages in this arrangement. As a result of increasing x the gape of the mouth will correspondingly decrease. However, De Mar & Barghusen (1973: 626) state: 'If the increase in relative lengths of the moment arms achieved by increasing y and increasing x are the same, the increase in distance that the muscle must stretch to achieve a given gape is the same for the two methods. Thus . . . reduction of gape is the same and not a consideration *per se* in making the comparison.'

Secondly, Ostrom (1964) indicates that because of their vertical orientation the origin of the adductor fibres would encroach on to the facial region, restricting their size and power. This statement is true except in cases where the orbit is anteriorly placed or decreased in size, making it possible to extend the temporal origin of the jaw adductors anteriorly. In *Typhlosaurus* the eye is degenerate and lacks eye muscles. The orbit is consequently reduced and the temporal region elongated. The lateral downgrowth of the parietal and the forward extension of the anterior superior process of the pro-otic makes additional areas of origin available for the adductor musculature, compensating for the loss of such structures as the supratemporal arch. The relatively forward position, therefore, of the adductor muscles suggests a difference in the line of muscle action as compared to a non-fossorial skink like *Mabuia*.

From the work of De Mar & Barghusen (1973) it is clear that the height and position of the coronoid process is influenced by the line of muscle action. Any difference, therefore, in the line of muscle action would be reflected in the proportions of the lower jaw.

In comparing the lower jaws of *Typhlosaurus* and *Mabuia* the outstanding feature is their proportional similarity in terms of x and y . The tooth row, however, is shorter in *Typhlosaurus* than in *Mabuia* because of the subterminal mouth of the former. Consequently, the force of the bite at the jaw symphysis will probably be proportionately greater in *Typhlosaurus* than in *Mabuia*. The similarity of the two lower jaws suggests that the mean line of muscle action is identical in both forms, and that there is probably no difference of any consequence in the action of the jaw.

It therefore appears that the primary adaptation for a fossorial habit is streamlining of the body and its various parts. Loss of limbs and attenuation of the body is associated with the new mode of locomotion. Strengthening of the skull for burrowing results in the lateral downgrowth of the parietal bone and the extension of the anterior superior process of the pro-otic bone, the lengthening of the temporal region, and the loss of metakinesis and the supratemporal arch.

It may be concluded therefore that the distribution of the jaw muscles in *Typhlosaurus* represents the optimal functional arrangement to maintain a

mode of jaw action essentially similar to that of a non-fossorial lizard such as *Mabuia capensis*, within a skull that is proportionally different because of marked changes resulting from a fossorial mode of life.

ACKNOWLEDGEMENTS

I wish to thank the following persons: Professor M. E. Malan of the Zoological Institute of the University of Stellenbosch, who suggested the project, for her guidance and assistance during the research; Dr M.A. Cluver of the South African Museum for critically reading the manuscript; Messrs M. N. Bester, A. J. Lindvelt, D. J. van Eeden, D. P. Mostert and Mrs R. Semmellink, all of the Zoological Institute at Stellenbosch for assistance rendered at various stages of the work; Mrs I. Chesselet of the South African Museum, her family and Mr P. J. Louw of Klein Botrivier for their fieldwork; Mr N. J. Eden of the South African Museum for taking the photographs; Miss A. E. Louw and Mrs P. D. Eedes for helping with the typing, and my wife Lorna for her valued assistance.

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*Not seen in the original.

ABBREVIATIONS

ac	anterior process of the coronoid
aem	m. adductor mandibulae externus medius
aep	m. adductor mandibulae externus profundus
aes	m. adductor mandibulae externus superficialis
aip	anterior inferior process of the pro-otic
ap	m. adductor mandibulae posterior
ar	articular
asp	anterior superior process of the pro-otic
at	stapedial artery
ba	bodenaponeurosis
bc	buccal cavity
bl	buccal lining
bo	basioccipital
bp	basipterygoid process
br	brain
bt	basal tuberosity
c	coronoid
cc	m. constrictor colli
ci	internal carotid artery
cm	m. cervicomandibularis
cp	coronoid process
d	dentary
dma	anterior portion of the m. depressor mandibulae
dmp	posterior portion of the m. depressor mandibulae
e	eye
em	m. episternocleidomastoideus
ex	extracolumella
gg	Gasserian ganglion
ggl	m. genioglossus
ghl	m. geniohyoideus lateralis
ghm	m. geniohyoideus medialis
gp	groove for the insertion of the pseudotemporalis muscle
fa	fascia supporting the extracolumella anteriorly
f	pad of fibrocartilage
fc	foramen for the chorda tympani
hg	m. hyoglossus
ia	m. intermandibularis anterior
if	infraorbital fenestra
ip	m. intermandibularis posterior
it	insertional tendon of the m. cervicomandibularis
itp	insertional tendon of the m. pterygoideus
lb	lateral lamina of the bodenaponeurosis
lc	m. longus colli
lca	m. longissimus capitis
lce	m. longissimus cervicis
ll	longitudinal lingual fibres
lp	m. levator pterygoidei
lq	lateral lamina of the quadrate tendon
ls	lateral semicircular canal
lv	lateral head vein
m	musculus
mb	medial lamina of the bodenaponeurosis
me	Meckelian cartilage
mq	medial lamina of the quadrate tendon
ms	lateral mandibular shelf
nl	nuchal ligament
oc	m. obliquus capitis magnus

oe	fused ophistotic-exoccipital
p	m. pseudotemporalis
pa	pre-articular
pal	palatine
par	parietal
pat	ascending process of the tectum synoticum
pb	parasphenoid—basisphenoid
pc	posterior process of the coronoid
pd	tendinous pad on m. pterygoideus
pe	lingual process
pf	postfrontal
pm	posterior mylohyoid foramen
pn	palatine nerve
po	pro-otic
prp	m. protractor pterygoidei
pt	pterygoid
pts	m. pterygoideus
q	quadrate
qa	quadrate tendon
r	rostral
ra	m. rectus capitis anterior
rm	mandibular ramus of V
rma	maxillary ramus of V
rop	ophthalmic ramus of V
rp	m. rectus capitis posterior
s	stapes
sa	surangular
sc	spinalis capitis
sd	m. spinalis dorsi
sp	splenial
sq	squamosal
st	supratemporal
t	tendinous sheath of the extra columella
tc	tendinous connection between supratemporal and quadrate
tl	transverse lingual fibres
to	tongue
tr	trachea
ts	tendon between the squamosal and quadrate
vb	vertical lamina of the bodenaponeurosis
vl	vertical lingual fibres
vq	vertical lamina of the quadrate tendon

6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. n., sp. n., comb. n., syn. n., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).

Nucula largillierii Philippi, 1861: 87

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and of date.

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text

e.g. '... the Figure depicting *C. namacolus* ...'

'... in *C. namacolus* (Fig. 10) ...'

- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names

e.g. Du Toit but A. L. du Toit

Von Huene but F. von Huene

- (c) Scientific names, but not their vernacular derivatives

e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.



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JURI A. VAN DEN HEEVER
THE CRANIAL AND CERVICAL MUSCLES OF THE
SOUTH AFRICAN LIMBLESS LIZARD
TYPHLOSAURUS AURANTIACUS AURANTIACUS
PETERS (REPTILIA, SAURIA)